THE TEMPLE PRIMERS

PLANT GEOGRAPHY

By GEORGE S. BOULGER, F.L.S., Etc.
Honorary Professor of Natural History
in the Royal Agricultural College, Etc.

PLANT GEOGRAPHY

BY GEORGE S BOULGER F.L.S

ALDINE HOUSE
J. M. DENT & SONS LTD

1912 · 10-13 BEDFORD STREET, LONDON

THE TEMPLE PRESS, PRINTERS, LETCHWORTH.

PREFACE

The difficulty of treating a subject as wide as plant-geography within the compass of a primer is so obvious that it is hardly necessary to crave the reader's recognition of the limitations of space.

Originality is neither possible nor entirely desirable in a book of this character, and I hope that the brief Bibliography may be accepted in lieu of further acknowledgement of my indebtedness to others.

I wish, however, to take this opportunity of thanking those who have kindly assisted me by the loan of illustrations—Sir David Prain, F.R.S., by whose permission Figs. 2, 8, and 11 were copied from pictures in the Kew Museum; Dr. T. W. Woodhead and the Council of the Linnean Society for permission to use Fig. 3; Professor Herbertson and Mr. Edward Arnold for Fig. 5; the British Vegetation Committee and Mr. A. G. Tansley for Figs. 12-16; and Messrs. Quelle and Meyer, of Leipzig, for Figs. 1, 4, 6, 7, 9, and 10, from Professor Graebner's *Pflanzengeographie.*

G. S. BOULGER.

RICHMOND, *October* 1912.

CONTENTS

		PAGE
	INTRODUCTION	1

BOOK I

THE EVOLUTION OF THE PLANT-WORLD

CHAP.		
I.	The Distribution of Land and Water in the Past	7
II.	Climate in the Past	10
III.	The Time and Place of the Origin of Plant-life	13
IV.	Floras of the Past	14
V.	The Coming of our Modern Angiosperms	20

BOOK II

THE FACTORS OF DISTRIBUTION

I.	The Climatic Environment and the Response to it	27
II.	The Soil	45
III.	Organic Environment	55
IV.	Dispersal and Migration	62
V.	Physiographic Factors	70
VI.	Barriers	74
VII.	Insular Floras	78
VIII.	Bridges	82
IX.	Mountain Floras	86
X.	Water-plants	90

BOOK III

FLORISTIC REGIONS

I.	The Northern Zone	95
II.	The Tropical Zone	102
III.	The Southern Zone	112

BOOK IV

BOTANICAL ECOLOGY OR TOPOGRAPHY	122
BIBLIOGRAPHY	131
INDEX	133

LIST OF ILLUSTRATIONS

FIG.		PAG
1.	View on Kerguelen Island	4
2.	Mangrove-swamp near Goa	5
3.	Vertical Zonation	5
4.	Palm-tree drifting in the open sea	(
5.	Vegetation-zones of latitude and altitude . . .	7
6.	*Merope*, a Composite of the Higher Andes . . .	
7.	*Salix polaris* Wahl., the Dwarf Arctic Willow . .	
8.	*Rheum nobile* Hook. fil.	1
9.	Epiphytic Orchid (*Cattleya*) in Brazil	1
10.	Forest of Eucalyptus in West Australia . . .	11
11.	Grass-trees (*Xanthorrhea*), Cycads, and Ferns in West Australia	117
12.	Open reed swamp association	124
13.	Oak-birch heath association	127
14.	Heath association invaded by *Pinus sylvestris* L. . .	127
15.	Dry Oak-wood on sandy loam	129
16.	Interior of Beech-wood on chalk	129

PLANT GEOGRAPHY

INTRODUCTION

THE recognised masterpieces of human art, whether in painting or in sculpture, are, almost all of them, representations of the human form. Most of the loveliest scenes of natural beauty, on the other hand, owe a large proportion of their charm to the aspects of plant life. The dark forest of northern pines, the crimson of the open heath, the willows by the stream, the gay meadow blossoms surrounded by Alpine snows, the slender, graceful palms of the tropics, or the tangled jungles of the equator have in this respect almost their only rivals in the grandeur of bare mountain peaks with their perennial snows, and in the ever-changing hues of ocean.

The art of the painter and the many modern books of travel have made the most stay-at-home among us familiar with the fact that the vegetation of one land is widely different from that of another. Even those without the wide knowledge of Macaulay's schoolboy know something of the absence of plant-life in the frozen North; of the stunted vegetation of the only less permanently frozen tundra; of the date palms of the African oases, the giant cone-bearing trees of western North America, the gum trees of Australia, and the rope-like lianas and the orchids on the boughs of the many huge trees in the steaming atmosphere of what is termed the "zone of constant precipitation." Now that the Swiss Alps have become recognised as the playground of Europe, many who have seldom, if ever, given a thought to such a subject as botanical geography must have noticed the gradual disappearance of the wild and cultivated trees and other plants of the valley as the ascent of a mountain is made, firs succeeding the oaks, chestnuts, and walnuts, until the upper limit of all trees is reached, and ultimately only a few lichens cover the rocks near the line of perpetual snow.

There is thus a vague general recognition of the fact that vegetation varies with latitude and with altitude, accompanied by the inevitable corollary that this distribution of plant life must be largely dependent upon climate. A closer attention to the facts will convince us that, true as this conclusion is, it is by no means the whole truth. If it were so, we might expect, for instance, that distant lands with practically identical climates would bear practically identical vegetation; whereas what we find is, not identity, but a certain resemblance, or, as it is termed, representation.

Those who own gardens with glass houses, or who are familiar with our large botanical gardens, will recognise in the classification of cultivated plants into such groups as "hardy," "half-hardy," "greenhouse," and "stove" plants the same dependence of the life of certain kinds or "species," as the botanist calls them, upon heat, or, at least, upon the exclusion of frost; and will probably also notice that the presence or absence of moisture plays an almost equally important part in their successful cultivation.

The student of geography soon becomes aware of the vast importance of vegetation in human affairs. Dense forests, barren deserts, or undrained marshes have always necessarily been thinly peopled. Man, especially in the earlier stages of civilisation, is largely dependent on the crops he can grow in the cleared, drained, and tilled land in his immediate neighbourhood. The wild spices he may collect in the forest of the tropics, or the surplus produce of his fields, may be the foundation of international commerce. Pasturage for cattle, timber for shipbuilding, or a soil suitable for the growth of some particular plant, whether valuable for food, fibre, medicine, or what not, may largely determine the distribution of population or industries within the individual state. The reckless destruction of some wild species which is a source of wealth may prove the commercial ruin of a district; while its careful conservation may mean prolonged economic progress; and the introduction of some foreign plant into a region suitable in climate and soil for its cultivation may give a fresh start of prosperity to a land previously but sparsely peopled.

The intellectual justification of modern botanical

study is not, however, mainly or directly economic: it is biological. The structure of plants is chiefly considered with reference to their functions as living beings, *i.e.* physiologically, unless it is viewed merely as an indication of greater or less affinity with other plants, and thus as a clue to their evolutionary ancestry. The life of the individual plant is recognised as a function of two variables, viz. the characters which it inherits from its parents, and the result upon its development of its environment. This environment does not consist wholly in climate and soil, although these are factors of supreme importance. The plant will require a certain amount of heat to sprout, to flower, or to ripen seed: it will require a certain amount of moisture in the soil and some small modicum of soluble saline substances also available at its roots: its healthy development will be influenced by its exposure to light and wind; but its existence may be also conditioned by other living beings, either plants or animals. As a seed about to sprout, as a delicate slender seedling, or even at a much later and more robust stage of its life, the occupation of the surrounding soil by other plants, or the shade of their overhanging foliage, may prove fatal to it. Substances not otherwise available, or even harmful, to its roots may be rendered useful if certain bacteria exist in the soil to set up suitable processes of fermentation. The fertilisation of its seeds may depend upon the conveyance of its pollen from one flower to another by the agency of insects; while the dispersal of its seeds to spots where they may be freer from competition may depend on their being carried by birds or entangled in the hair of passing animals.

The presence of any plant in any one place, moreover, does not depend solely on the suitability of that place for that species of plant. Climate and soil may be suitable: there may be unoccupied ground; and all necessary organic environment may also be present; but in some manner or other, whether as seed or spore or growing plant, the species must reach this suitable spot. It must either be transported from some other spot, near or far, where it has come into being; or it must have originated *de novo* in the area where we now find it.

As vegetable physiology considers alike the external

causes which act upon plants, and the response that the plants make in function and structure to such causes, so botanical geography has to do both with the causes and the results of the distribution of plants. Such a study has, as has been suggested, its interest for the artist, the traveller, the scientific geographer, the man of commerce interested in the sources of industrial produce, the horticulturist, and the botanist. As a department of scientific inquiry, however, its main importance is biological. It is part of the more general science of the distribution of living beings; and, to some extent, the laws governing the distribution of plants apply also to that of animals. It is these general principles that are of the greatest interest to the student of science. The way in which one or more species of plants have reached a particular area is more important to him than the fact that they have done so, far more important than the economic uses to which they may be put. Treating the subject as a branch of natural history, he may almost ignore those changes in distribution that man has intentionally produced, the introduction of agricultural plants into new lands, and the appropriation of huge areas for the cultivation of a few valued species, such as the cereals, the pasture grasses, cotton and other textile substances, etc. Man's involuntary dispersive action, on the other hand, must be taken into consideration along with that of other animals.

Whilst it is obvious that the present distribution of land and water over the surface of the globe must profoundly affect the areas occupied by land plants and by marine algæ, as well as the present distribution of temperature, rainfall, etc., a slight knowledge of geology will enable us to appreciate the fact that this distribution of land and water has not always been the same. Any description of the present distribution of plants, dependent as it must be upon present geographical conditions, can only be temporarily true. These geographical conditions and their biological results have not always been the same; nor will they remain as they are. The "natural floras," or assemblages of associated plants, of to-day are only of to-day, and we must not ignore the influence of former conditions and changes in the distribution of land and water. Fragmentary

as is the evidence, our existing vegetation can be linked with that of past geological periods: its existing distribution is that of the vegetation of the past, modified by changes in the environment perhaps as profound as those seen in the vegetation itself.

During the second half of the nineteenth century the division of the earth's surface into climatic regions of vegetation was, by the labours of many scientific travellers, very fully accomplished. Species were tabulated according to their distribution, and, under the influence of the theory of evolution, it was recognised that neighbouring natural floras are connected together by the migration of species from one to another; and also distinguished from one another by peculiar or "endemic" species which have originated where they occur by the modification of pre-existing forms. This department of the subject has been termed "floristic geography," and deals, it should be noted, mainly with the distribution of species over large areas.

During the present century the attention of botanists has been more directed to the simultaneous relation of groups of plants (united only in physiological requirements and not generally by genetic affinity) to their "habitats" or situations as regards soil, drainage, aspect, etc. This study of the homes of plants is termed "ecology"; and this treatment of plants, in groups presenting marked landscape or "physiognomic" characters according to their habitat, has been termed "ecological geography"; but might rather perhaps be named "ecological topography." It deals with vegetation rather than with individual species; and, though much concerned with such local climatic influences as those due to slope, aspect, and drainage, treats more of plant physiology than of what is usually considered as geography.

If then we take Phyto-geography, or the geography of plants, to signify the science of the distribution of plant-life over the surface of the globe, we shall deal with it under four heads. We shall first sketch briefly what is known as the evolution of the plant-world and its distribution in past geological periods. Secondly, we shall write of the factors of distribution:—climate, soil, the effects of other plants and animals, the response of plants to these influences, the agencies and mechanisms

for dispersal, the barriers to migration, and how they have been surmounted. Thirdly, the floristic regions of the globe will be briefly described; and, lastly, the chief ecological groups will be discussed. Some elementary knowledge of botany and geography must be assumed; and it is obvious that, within the compass of a little book like the present, no part of so wide a subject can well be treated at all completely. The whole book is but an introduction; but the author hopes soon to issue a more comprehensive work in which each division of the science can be dealt with more fully. More space has intentionally been devoted to the causes than to the results of distribution.

BOOK I

THE EVOLUTION OF THE PLANT-WORLD

CHAPTER I

THE DISTRIBUTION OF LAND AND WATER IN THE PAST

Our earth is a somewhat irregular spheroid, the surface of which is estimated at 196,940,000 square miles. Of this about 142,000,000 square miles is now sea, and 55,000,000 land, *i.e.* about 71.7 per cent. of the former to 28.3 per cent. of the latter; or roughly as 5 : 2. A glance at the map, or, still better, at a globe, shows how very unequally this land and water is at present distributed over the surface of the globe. There is, in fact, thirteen times more land north of the equator than there is to the south of it. This alone must obviously have a profound influence on plant-distribution—the vast ocean area being almost exclusively represented, so far as plant life is concerned, by Diatoms and Algæ; very few flowering plants, such as the Grass-wracks (*Zostera*), inhabiting salt water.

Though at first sight the disposition of the masses of land and water on the present surface of the globe appears most irregular, it will be readily perceived that there is an Arctic or North Polar Ocean surrounded by an almost continuous ring of land which is continued in three pairs of continents that extend meridionally and taper to the south. Similarly, round the land of the Antarctic Continent there is a continuous belt of ocean extending northwards in three oceans tapering in that direction, two of them uniting in the Arctic. Land and water are thus, as it has been said, " arranged like a pair of interlocking cog-wheels, each with three teeth." It will also be observed that the land and water areas on the surface of the globe are to a very

great degree antipodal to one another, the Arctic Ocean corresponding to the Antarctic Continent, Europe and Africa to the South and North Pacific, North America to the South Indian Ocean, and Australia to the North Atlantic. These salient facts of distribution agree well with an interesting hypothesis of the origin of the surface features of our globe, the latter part of which was first put forward by an American writer, Mr. W. Lowthian Green.

Many facts in astronomy, and especially the results of the examination of the light of heavenly bodies with the spectroscope, lend support to what is known as the nebular hypothesis of the origin of our earth in common with the rest of the solar system. According to this hypothesis the solar system has resulted from the gradual cooling and condensation of a nebula composed either of incandescent gas, or, more probably, of swarms of meteorites constantly colliding with one another and passing into a vaporous condition. This nebula, condensing towards its centre, would throw off, or leave behind, successive rings of progressively heavier matter which, by disruption, have condensed into planets, of which our earth is one. Similarly, it is thought, the rupture of each such planetary ring would so raise the temperature of the resultant planet as to vaporise it, and allow the vapours to arrange themselves and condense in successive shells of densities increasing towards its centre. Lowthian Green's tetrahedral theory is that the earth, originating in the manner just indicated, would be approximately spherical, the sphere being the geometrical form which combines the maximum of volume with the minimum of surface; and that, in further contraction on cooling, it would tend towards that geometrical form which combines the maximum of surface with the minimum of volume, viz. the tetrahedron. The tetrahedron is enclosed by four equal and similar triangles; and the theory associates the four oceans with the four faces of this form, and the circumpolar ring of land and the three pairs of continents with its edges, the face represented by the Arctic Ocean having as its antipodes the solid angle represented by the Antarctic Continent. The spherical earth is, in fact, supposed to have undergone a tetrahedral deformation, sagging on the four sides, or faces, which have produced

the ocean basins. The facts of the earth's form are shown to be still more in accordance with this theory in comparison with a form, intermediate between the sphere and the tetrahedron, known in geometry as the hexakistetrahedron, or six-faced tetrahedron, which may be described as a tetrahedron with a low pyramid of six triangular faces on each of its four sides.

The present distribution of land and water agrees very closely with the requirements of this hypothesis; but it is more important that the primitive distribution should be shown to do so. Most of the present land surface can be shown, by its rocks and their contained fossil remains, to have been at one period or another beneath the sea, though not all at one time. It may, however, be true that most of the sedimentary rocks are of shallow water origin, and have not originated in such abyssal depths as those of our present ocean-bed. From this it will follow that, though subject to repeated oscillations, so that one tract after another has disappeared and reappeared from beneath the sea, the continents, though constantly varying in shape and size, have in the main retained their individuality, and the existing ocean basins have been, perhaps from the very beginning, great trough-like depressions of the earth's crust. Such a belief in the permanence of at least the skeletons of our continents and of the deeper parts of the ocean as land and water respectively is compatible with the admission of great changes linking land-masses now separate, or *vice versâ*. Thus, there is considerable evidence of former extensions of land, at different periods, between Scandinavia, the Highlands of Scotland, and Donegal; between the mainland of Manchuria, Saghalien, and Japan; and between the south-west of South America and the adjacent islands. Some evidence, however, points to the former existence of land-masses which can hardly be in any way considered as extensions of our present continents. Thus there is much geological evidence of the connection in a remote geological period of the Scandinavian area mentioned above with North America and Greenland in a continental mass named *Arctis;* and at a later date, lasting from the Coal-Measure period at least to that known to geologists as Permian, of the union of Brazil, Argentina, and the Falkland Islands with Africa south

of the Tropic of Cancer, Madagascar, Arabia, Southern India, Australia, and Tasmania in another vast continental area known as *Gondwanaland*. Possibly the rigidity of these two ancient land-masses in the shrinking crust of the earth may have produced the folding of the more sedimentary rocks of the area between them, giving rise to those systems of "fold-mountains" which form the axes of our existing continents. Although Gondwanaland seems to have been broken up by the subsidence of the areas now occupied by the South Atlantic and Indian Oceans, a possible continuation to a later period of some southern connection between South America and Australasia, perhaps by way of the Antarctic Continent, may serve to explain some difficulties in the present distribution of plants and animals.

Such a minor difference in the distribution of land and water as the union of the British Isles to the Continent of Europe both eastward and south-westward, involving as it does but a slight difference in the relative levels of land and ocean, has certainly occurred within far more recent times than the differences just referred to.

Though most of our existing species of plants, and even many larger groups, are of so modern a date, geologically speaking, as to have originated independently of the more ancient distributions of land and water, we may trace the influence of these last in the origin and dispersion of some of the main divisions of the plant-world. As we shall see, however, it is extremely difficult to do this with any certainty.

CHAPTER II

CLIMATE IN THE PAST

THE term climate referred originally to what we term the sun's altitude, or the angle at which the sun's rays fall upon various parts of the earth's surface. The earth's axis of rotation, the line joining the North and South Poles, is inclined $23\frac{1}{2}°$ towards the plane of its orbit or path round the sun, which plane is termed the ecliptic, *i.e.* it makes with that plane an angle of $66\frac{1}{2}°$. As a consequence of this inclination the sun is vertical

over the equator, or great circle midway between the poles, twice in the year, viz. at the spring and autumn equinoxes. At those seasons the "circle of illumination," or great circle dividing day from night, will pass through the poles, so that day and night will be equal, *i.e.* twelve hours each, everywhere. At other seasons they will be equal only on the equator, which is, therefore, termed the equinoctial line, their inequality increasing with the latitude, *i.e.* towards the poles, where we have practically a day and night each of six months' duration. Not only does the difference between day and night increase with the latitude, owing to this inclination of the earth's axis, but the sun's altitude, or the angle which its noon position makes with the horizon, diminishes, from the same cause, towards the poles. Only within 23½° of the equator is it ever vertical. Only within 23½° of the poles does it ever remain for twenty-four hours or more above or below the horizon. Thus this inclination of the earth's axis gives us the difference between the length of day and night at different times of the year, and the consequent seasonal variations in the heat and light received during any part of the year by any latitudinal zone of the earth's surface. Incidentally, too, it may be remarked that upon these variations in the heat received from the sun depends, in the main, the rate of evaporation of water and, as a consequence, to a great extent, the amount of its precipitation, *i.e.* of the rainfall.

Presuming this inclination of the earth's axis to have been the same, or nearly the same, in past ages as it now is, and the equator and the poles to have occupied the same position on the surface of the globe as they do at present, there will always have been an area of cold round about each pole, and a zone of great heat midway between them. Such an equatorial belt of extreme heat will form a serious barrier against the migration of plants adapted to a milder climate from the Northern to the Southern Hemisphere, or *vice versâ*, at the sea-level. It must, however, be borne in mind that as we ascend from sea-level to higher altitudes—no matter in what part of the world—though the duration of day and night remain the same, the temperature, or sensible heat of the air, which is mainly derived from radiation from the earth, gradually diminishes. At the present

day, except in the case of the slow-cooling lavas of volcanic regions, or the neighbourhood of hot springs, we need not consider the heated interior of the earth as contributing to the temperature of the air; but can attribute this entirely to the direct, or reflected, heat of the sun.

During the earlier portion of the history of the plant-world of which we have any satisfactory records, however, this may not have been the case. There is among the oldest well-known fossil plants, those of the rocks below the Coal-Measures, so great a uniformity, no matter from what part of the world they may have been collected, as to suggest one world-wide, or well-nigh world-wide, climate which may have been owing to the then operative and unradiated primitive heat of the globe.

This Lower Carboniferous Flora is followed in the Southern Hemisphere by evidence of extreme and wide-spread conditions of great cold, which seems to have spread northwards, and to have produced a marked change in the vegetation, which also extended northward, so that representatives of the southern cold conditions mingle with descendants of those of the earlier hot conditions.

In yet more modern times, geologically speaking, there is again a restored uniformity of vegetation in Jurassic times almost as marked as that of the Lower Carboniferous. Again, in far more recent times—times little, if at all, antedating the advent of man upon the earth—there is proof of the existence in the Northern Hemisphere of extreme cold extending far south of the Arctic Circle, and lasting for a long, though apparently intermittent, period; so that vegetation may well have been driven to migrate southwards, to return, more or less, as the cold abated.

We cannot, therefore, assume that either the distribution of land and water, or that of climate, have in past ages been the same as they are at present.

CHAPTER III

THE TIME AND PLACE OF THE ORIGIN OF PLANT-LIFE

We know little, or nothing, as to the period of the origin of plant-life.

Among the oldest rocks that are probably of sedimentary origin, the Laurentian of Canada, there occur beds of graphite, or mineral carbon, destitute of all organic structure, which may be of vegetable origin. In more modern strata, still of immeasurable antiquity,—the Cambrian,—ripple-marks, the tracks of animals, and crystalline layers recalling the "frost trees" of our window-panes have been erroneously described as seaweeds. In the later Ordovian and Silurian series more precisely recognisable traces of Algæ are found, some of considerable size and of comparatively advanced organisation, suggesting that among marine plants, as among land plants, which make their first appearance in the Devonian period, a long evolutionary history has been lost in the metamorphosed rocks of preceding ages. That the earliest known fossil plants, and, in fact, all those certainly older than the Devonian period, are Algæ may be owing to our knowledge of the sedimentary rocks of those early ages being confined to marine deposits. It agrees, however, with much evidence, derived from structure, pointing to that group as the first to be evolved in the history of the plant-world. As it has been suggested that animal life originated in shallow sea-water near shore, so, perhaps, did that plant life which most probably had its beginning about the same time as, or somewhat before, the animal world.

We have as little definite knowledge with regard to the place of origin of the plant-world as we have with reference to its period. The brilliant suggestion of Buffon that the earth in cooling would cool first at its poles, and that life, therefore, probably originated at the North Pole, and then migrated southward in successive dispersing hordes, belongs to a time when it was not realised that the origin of life dated back to a remote past with a distribution of land and water very

different from the present; and that life itself was represented by successive groups of organisms also very different, at least in their numerical proportions, from those of to-day. Not only is there no *à priori* reason against the South Pole being also a centre of origin and dispersal; but it is, perhaps, more probable that life should have originated in the hot, moist climate of equatorial regions where it is seen to-day in its most prolific luxuriance than in the more frigid neighbourhood of either pole. We know nothing, however, as to the relation in time between the primitive cooling of the globe and this first appearance of life upon it.

CHAPTER IV

FLORAS OF THE PAST

FRAGMENTARY as is the evidence, it is now apparent that the story of the evolution of plant-life is continuous. We cannot, it is true, trace among fossil plants a passage from Algæ to Bryophyta, or from Bryophyta to Pteridophyta. We have, in fact, little, if any, evidence of the existence of mosses in Palæozoic times. They might be supposed to have contributed an important element in the vegetation of the warm, moist land-surfaces of Carboniferous times; but, in spite of the fine state of preservation of many equally delicate plant structures from that age, they are hardly represented. Among Vascular plants, however, there is a distinct and continuous succession from Devonian times to the present day.

Although in the Devonian rocks all the main existing divisions of the Pteridophyta, viz. Horsetails, Ferns, and Club-mosses, and a primitive group of Gymnosperms (*Cordaïtes*) have already made their appearance on the earth, there is evidence of the existence in that age of generalised types, combining the characters of several groups and thus suggesting their ancestral character. In later series of rocks other groups of Gymnosperms appear, followed in Cretaceous times by Angiosperms. Nor are the undoubted facts of degeneration within these various groups in the least a contradiction of

the general evolutionary advance. "The palæobotanical record is essentially the story of the successive ascendency of a series of dominant families, each of which attained its maximum in organisation as well as in extent, and then sank into comparative obscurity, giving place to other families which, under new conditions, were better able to take a leading place. As each family ran its downward course, its members either underwent an actual reduction in structure as they became relegated to herbaceous or, perhaps, aquatic life, . . . or the higher branches of the family were crowded out altogether, and only the 'poor relations' were able to maintain their position by evading the competition of the ascendant races."[1]

This succession of dominant groups was well tabulated by Brongniart in 1849 as follows:—

III. Reign of Angiosperms	6. Tertiary epoch. 5. Cretaceous epoch.
II. Reign of Gymnosperms	4. Jurassic epoch (including the Wealden) 3. Triassic epoch.
I. Reign of Acrogens	2. Permian epoch. 1. Carboniferous epoch.

The flora of the Devonian age, the oldest known land flora, described chiefly from North America, does not differ very widely from that of the overlying Lower Carboniferous. Not only does it include undoubted horsetails, such as *Archæocalamites;* club-mosses, such as *Lepidodendron:* and apparently true ferns, such as *Archæopteris;* but also three or four generalised types of great interest.

In Upper Devonian rocks, in Bear Island in the Arctic Ocean, a genus has been discovered known as *Pseudobornia*. It was a large plant with a jointed stem like *Calamites*, but with much-forked, divided, and almost fern-like leaves in whorls of about four each. In the same rocks, but also elsewhere and in more modern beds of Carboniferous age, we have the better-known genus *Sphenophyllum*, which is the type of a distinct class of Pteridophyta. These were slender,

[1] D. H. Scott in *Darwin and Modern Science* (1909), pp. 202-3.

possibly climbing, plants with jointed stems, long ribbed internodes, and broadly wedge-shaped leaves in whorls generally of six, sometimes so divided as to appear as distinct leaves. Their fructification was, in general, a cone resembling that of *Calamites;* and undoubtedly the *Sphenophyllales* suggest a common ancestry with the *Equisetales;* whilst *Pseudobornia* not only confirms this community of descent, but also suggests that ferns may have had a closely related origin.

The Club-mosses are a more isolated class; and, while at the present day they are divided into types, such as *Lycopodium*, with only one kind of spore, and those with two, such as *Selaginella* and *Isoëtes*, in Palæozoic rocks every known form is like these last, "heterosporous." The group as a whole seems not only to have dwindled in the size of its members, but also to have undergone structural degeneration. This, however, did not begin until a later period.

Other fern-like leaves occur in Devonian rocks, described as *Neuropteris, Alethopteris*, etc. Recent work, however, has shown not only that these leaves were connected with large woody stems, formerly believed to be coniferous, but now seen to resemble that of the Cycads, but also that they bore true seeds and pollen-grains approximating in structure to those of Cycads. These plants are now, therefore, referred to a group, known as *Pteridospermeæ*, which we must apparently consider as gymnospermous rather than pteridophytic.

Lastly, we have in Devonian rocks leaves attributable to the *Cordaïteæ*. These were lofty trees, sometimes 100 feet high, branching above and bearing simple leaves, sometimes three feet in length and five inches wide. In foliage and wood they resembled the broad-leaved *Araucarieæ* of the Southern Hemisphere of to-day; but they had a large discoid pith like that of the walnut. They had male catkins of erect stamens bearing from four to six pollen-sacs and protected by bracts, and similar groups of fewer ovules resembling those of *Pteridospermeæ* and *Cycadeæ*. Related as this prominent group undoubtedly is both to these classes and to *Coniferæ*, it is most closely represented to-day by that curiously isolated type the Maidenhair-tree (*Ginkgo biloba* L.) of China.

The widespread and luxuriant flora of the Coal-Measures seems to have differed little in general characters from that of the Devonian period. Whole beds of coal are formed of the leaves of *Cordaïtes*. *Lepidodendron*, that genus of gigantic club-mosses which finds, perhaps, its nearest living representative in the humble aquatic *Isoëtes*, is one of the best known of Coal-Measure fossils, with its ally *Sigillaria* and the giant horsetails, *Calamites;* while it is now recognised that the majority of the so-called fern fronds belong to the *Pteridospermeæ*. At the same time, we have specimens from our English Coal-Measures of undoubted ferns, the sporangia of which are destitute of an annulus, while the stele (or vascular axis of their leaf-stalks) is markedly H-shaped in transverse section. For these generalised types, combining characters of the *Ophioglossaceæ*, *Osmundaceæ*, and *Marattiaceæ*, the name *Primofilices* has been suggested. In spite of the proof that many sporangia supposed to belong to ferns are truly the microsporangia, or pollen-sacs, of *Pteridospermeæ*, it is possible that true *Marattiaceæ*, ferns with stipules at the base of their smooth-stalked, much-divided fronds, with a complex stem-structure, and with their sporangia united in "synangia," did contribute to our Coal flora.

The club-mosses, though represented by gigantic tree-like forms, the stems of which had that power of increasing in diameter by secondary growth once thought peculiar to flowering plants, also included herbaceous forms as small as their modern representatives. Some of these, such as *Miadesmia*, in spite of their reduced size, exhibit a great advance in the evolution of their reproductive system — producing true seeds — though in other characters closely resembling *Selaginella*.

It is possible that true Conifers and Cycads may be represented in European Carboniferous rocks by such fossils as *Ullmannia*, *Noëggerathia*, and *Pterophyllum;* and the coniferous nature of the Permian *Walchia* is unquestioned.

Obviously the flora of the Palæozoic age was not exclusively cryptogamic; although, perhaps, many of its primitive seed-bearing plants, like *Ginkgo* and the Cycads to-day, may have retained that relic of an aquatic ancestry, the spirally-coiled spermatozoid within the pollen-tube.

The second great vascular flora, though often termed Mesozoic, in its origin overlaps, or is continuous with, that first great "Reign of Acrogens" with which we have been dealing. It differs in the proportion that one group bears to another, besides being characterised by advance and increasing variety in groups that had appeared earlier, although by degeneration in others. Its origin and centre of dispersion would seem to be more definitely traceable than that of the Palæozoic flora, to be apparently southern. Here we first meet with evidence of a division of the earth's surface into distinct biological regions.

While much of North America, Central Europe, and Central Asia was apparently occupied, during the later half of the Carboniferous age, by low-lying, moist, forest-clad areas sinking intermittently below shallow seas, there is stratigraphical as well as palæobotanical evidence that an enormous continental area was forming to the south of the Tropic of Cancer, which seems to have remained continuous into Rhætic, if not into somewhat later, times. The Lower Carboniferous or "Culm" flora—or, as perhaps it should be designated, the Devoniano-Carboniferous flora—with its abundance of Lepidodendra, is found in the south as in the north. Thus there is evidence that the vegetation of the world was then singularly uniform. But from the latter part of the Carboniferous era Africa south of the northern tropic seems to have been united to Madagascar and India in a vast and elevated continental area, seeing that in large central and southern lake-areas no less than 18,000 feet of "Karroo beds" were laid down. The beginning of the period would seem to have been marked by intense glaciation; and such conditions have been traced for the same period in Brazil, the Argentine, the Falkland Islands, Tasmania, Victoria, New South Wales, and Queensland. This is represented by the great basal boulder-beds known in the various continents as the Dwyka Conglomerate, the Talchir beds, and the Bacchus Marsh beds. Above these come great thicknesses of strata destitute of marine shells, but containing plant-remains and other indications of land and freshwater conditions. To these beds, the approximate age of which is indicated by the term "Permo-Carboniferous," the name Gondwana system is applied, from

their development in Southern India, the whole vast continent which they indicate being known as Gondwana-land. Their flora is marked by the absence of *Calamites*, and, in India, of *Sigillaria* and *Lepidodendron*, the former being apparently replaced by *Phyllotheca* and *Schizoneura*, a distinct type of *Equisetales;* and the presence of *Sphenopteris* and *Pecopteris*,—probably *Pteridosperms*,—the more obviously cycadean *Pterophyllum*, and, above all, the abundant *Glossopteris* and *Gangamopteris*. *Glossopteris*, which has given its name to this entire flora, has a rhizome described under the name *Vertebraria*, bearing long, lanceolate or spathulate foliage-leaves with a midrib and anastomosing lateral veins, and smaller scale-leaves associated with sporangia and possibly sporophylls. *Gangamopteris* seems to differ mainly in the absence of the midrib. The sporangia may prove to be the microsporangia or pollen-sacs of a cycadeous plant, and these two abundant genera may thus prove to belong either to that characteristically Mesozoic class the *Cycadeæ*, or to its forerunner, the *Pteridospermeæ*.

While there is no clear evidence of true Cycads or members of our existing families of *Coniferæ* in Carboniferous rocks, a change in the general character of the vegetation seems thus to have begun in this southern continent earlier than in the north, and to have extended northward into China and Perm. The main divisions of the Cryptogamia and Gymnospermia seem to entirely antedate our existing system of continents.

In Secondary or Mesozoic rocks Club-mosses, Horsetails and Marattiaceous ferns play quite a subordinate part. The *Osmundaceæ* and forms related to *Gleichenia* and to the Malayan *Matonia* and *Dipteris* become prominent; but not the *Polypodiaceæ*. *Baiera*, and *Ginkgo* itself, represented, from Triassic times, over almost the whole globe, the Maidenhair-tree now so restricted in area. True Conifers, especially forms related to the broad-leaved *Araucarieæ* and *Agathis*, now entirely southern, become abundant. One plant in every three during Jurassic times seems, however, to have been a Cycad. The *Cycadophyta*, now represented by one family, the *Cycadaceæ*, comprising only nine genera and about 100 species, all southern, were then a varied and dominant group, almost as much so,

in fact, as are the Dicotyledons to-day. The remarkable type, *Bennettites*, Cycads bearing lateral flowers with spiral bracts, a whorl of compound pinnate staminal leaves with numerous pollen-sacs and stalked ovules developing into dicotyledonous exalbuminous seeds, occurs in the upper Gondwana series of India; while its abundant representation in Europe and North America is an instance of the uniformity that once again characterised the vegetation of the world in Lower Secondary times after the Permo-Carboniferous glaciation. Other Cycadophyta were so numerous, and of such world-wide distribution, that the name "Age of Cycads" is almost as appropriate as "Age of Gymnosperms" for the Triassic and Jurassic periods.

Not till after the deposition of our Wealden, or Lower and Middle Neocomian, beds does there seem to be any indication of the sudden advent and rapid advance of Brongniart's third "Reign," that of Angiosperms; nor is there any clear sign of the existence of botanical zones or regions.

As towards the close of the Palæozoic age, so towards that of the Mesozoic, the great change in vegetation antedates that in animal life and stratigraphical succession.

It is now generally agreed that a most probable ancestry for Angiosperms is to be looked for in the neighbourhood of Cycadophyta such as the early Mesozoic genus *Bennettites*. If so, it would follow that Dicotyledons, which are nearer in structure to the Cycads, would have been evolved before Monocotyledons. There is, in fact, much anatomical evidence that Monocotyledons are an early branch from the dicotyledonous ancestral stock; but there is little, if any, stratigraphical evidence of the one class having preceded the other.

CHAPTER V

THE COMING OF OUR MODERN ANGIOSPERMS

In point of numbers—including as they do more than 100,000 species—in size—including as they do the gigantic gum trees of Australia—in the area they cover, in variety of form and of adaptation to differing circumstances, the *Angiospermia*, or fruit-bearing Spermatophytes,

are undoubtedly the dominant type of vegetation to-day. Their attainment of this predominant position follows singularly soon, geologically speaking, upon the first evidence we have of their existence,

In the interior of the United States there is an enormous thickness of beds, mainly fresh-water and lacustrine, extending in age from Jurassic to Pliocene times, and in area from Long Island to Alabama and from the Mexican border to the Yukon. At the base of these is a series known as the Potomac formation, the lignites in which have yielded several successive assemblages of plants of the greatest possible interest. Unfortunately we have to rely for their affinities mainly upon the outline and veining of fragmentary fossil leaves. Of upwards of 700 named species, nearly half are described as Dicotyledons; but the leaf-characters seem also to clearly indicate the presence of Monocotyledons. The age of the lowest beds containing Angiosperms is apparently Neocomian (Lower Greensand), and leaves, also apparently belonging to Angiosperms, have been described from beds of similar age in Portugal and in England.

Higher in the Potomac series, in Upper Cretaceous beds, perhaps of Cenomanian (Upper Greensand) age, the Dicotyledons have attained a marked predominance, numbering 80 per cent. of the species, and comprising such genera as *Salix*, *Populus*, *Quercus*, *Juglans*, *Myrica*, *Magnolia*, *Liriodendron*, *Ficus*, *Sassafras*, *Eucalyptus*, *Acer*, *Ilex*, *Cæsalpinia*, *Bauhinia*, *Colutea*, *Aralia*, and *Andromeda*. These are mostly deciduous trees indicative of a warm temperate climate, and are so largely American as to show the continuity of the American flora to be greater than that of the European. *Gamopetalæ* are few and *Compositæ* absent. As Cenomanian plants have also been described from Greenland, comprising 30 Ferns, 8 Cycads, 27 Conifers, and 97 Dicotyledons, also suggesting warm temperate regions, we may say that this flora extends through 30° of latitude in the Northern Hemisphere, which gives rise to a probable inference that its centre of origin and dispersal was in this region.

In Saxony eight species of *Proteaceæ* have been described from beds of this age, and in Bohemia seventeen species of *Araliaceæ*, besides *Bombaceæ*, *Ebenaceæ*,

Mimoseæ, and others, suggesting a sub-tropical flora in Central Europe resembling that of Australia to-day. There is some indication of latitudinal zones at this period.

The coal-seams of the Laramie series, towards the close of the American Cretaceous, have yielded some 250 species, including palms, figs, oaks, poplars, planes, and magnolias in considerable variety, three species each of *Aralia*, *Rhus*, and *Sequoia*, besides *Ginkgo* and *Eucalyptus:* a list which perhaps suggests that there was then also a considerable divergence between the American and the European floras.

Passing to the lowest Eocene beds of Europe at Gelinden, near Liége, and in various places in France, we have oaks, chestnuts, laurels, Aralias, myrtles, bamboos, and fan-palms, a flora comparable to that of Southern Japan. In the Woolwich and Reading beds of Southern England planes, laurels, figs, *Robinia* and *Taxodium* suggest a sub-tropical climate and certainly present an American "facies," though the now Australian genus *Grevillea* also occurs. The drifted plant-remains in the overlying London clay are more tropical in character, including, with *Sequoia*, *Ginkgo*, and *Podocarpus*, oaks, *Liquidambar*, *Diospyros*, *Laurus*, *Eucalyptus*, fan-palms, and the fruits of *Nipa*, resembling those now carried down by the waters of the Ganges. Yet more tropical are the plants from the pipe-clays of the Bagshot series at Alum Bay and Bournemouth, comprising, as they do, *Cassia*, *Cæsalpinia*, *Dryandra*, *Eucalyptus*, palms, custard-apples, and a cactus.

The persistence of the American type of this flora in America, as compared with its disappearance in Europe, may be explained by the fact that, when unfavourable colder conditions set in, there were in America no barriers to a southward migration or to a northward return, the great fold-mountains of Secondary rocks running north and south; whilst in Europe the east and west mountains, Mediterranean Sea, both mainly of Tertiary origin, and, perhaps, the Sahara, did offer such insuperable barriers. Owing to the extermination of such genera as *Diospyros* and *Anona* our existing European flora is poorer in large fruits than that of America, or of our own area in earlier Tertiary times.

In Grinnell Land, in 81° N. lat., eleven conifers, an

elm, a *Viburnum*, a water-lily, and other species have been recorded, suggestive of the present climate 25° to the south; and in Disco Island (70° N. lat.), *Ginkgo*, *Platanus*, and *Sequoia*. It has been suggested that this temperate flora in Arctic latitudes belongs to the Eocene period, being more or less contemporaneous with tropical conditions in Central Europe, and that, subsequently migrating southward, it became the temperate Miocene flora of the latter area.

The isolation of existing provinces during Lower Eocene times is further illustrated by Australia, which had then a peculiar flora rich in *Proteaceæ*, *Myrtaceæ*, and *Amentaceæ*, and more related to the existing flora of that area than to those of other continents.

The Oligocene plants of the Hampshire Basin, including the coniferous *Arthrotaxis* now confined to Tasmania, and the ferns *Gleichenia* and *Lygodium*, suggest a climate somewhat cooler than that of the Bournemouth Eocene beds; as also do the abundant remains found in excellent preservation in the amber, or fossil resin of *Pinus succinifera*, belonging to this period, in the east of Prussia. These include several species of oak, chestnut, elder, and holly.

One of the best represented periods in the history of plants is the Upper Miocene, from which over 900 species have been recorded in Switzerland,—500 from one locality, Œningen near Lake Constance. These show a marked increase in the proportion that deciduous trees bear to the whole flora, with a decrease of palms and other tropical groups. Though there are 11 palms, the last Cycads to be recorded in Europe, a *Bromelia*, a *Zingiber*, several species of *Lygodium* and many other ferns, *Proteaceæ*, the American genus *Liriodendron*, and no less than 130 *Leguminosæ*, while Monocotyledons form a sixth of the whole flora, the presence of 94 *Cupressineæ* and 90 *Amentaceæ* indicate merely warm temperate conditions. Evergreen oaks, figs, and laurels were specially abundant; while from the evolutionary point of view it is interesting to note the complete absence of many orders of *Gamopetalæ*, such as *Campanulaceæ*, *Labiatæ*, *Solanaceæ*, and *Primulaceæ*, and the slight representation of *Compositæ* and others among the most highly organised.

During Pliocene times there is clear evidence of a

cooling down to conditions similar to those of the present day in Europe. In the earlier beds of this period in Central France an evergreen oak, *Laurus canariensis* Webb and Bert., and other species now confined to the Canary Islands, the Japanese *Torreya*, a *Buxus*, and a bamboo show kinship to the Miocene flora; as, perhaps, also do the earlier lignites in the Val d'Arno with such strikingly American genera as *Liquidambar*, *Persea*, *Carya*, and *Diospyros*, together with numerous oaks and pines. A later Pliocene deposit at Tegelen in the Netherlands shows an interesting approximation to that "Germanic" flora which now occupies the British Isles; but contains also the Grape Vine (*Vitis vinifera* L.) and *Pterocarya caucasica* C. A. Mey., now confined to the Caucasus, magnolias, suggestive of Japan, and an Indo-Chinese type of water-lily (*Euryale*), which plants would seem not to have been able to spread north-westward.

The Cromer Forest-bed, the last evidence we have of British vegetation before the setting in of the cold of the Glacial epoch, yields plant-remains which tell of a mild, moist climate, similar to that of England to-day, without either Arctic or South European forms, but including the Pine (*Pinus sylvestris* L.), the Spruce (*Picea excelsa* Link), and the Water-chestnut (*Trapa*).

While the Glossopteris flora of Gondwanaland was yielding place to the Mesozoic Cycadean and Araucarian assemblage it would seem that coralline limestones and other marine deposits were accumulating in the wider ancient Mediterranean Sea, or Tethys, that extended from Texas to Scotland, the Yenisei, the Irawadi, Egypt, and Java. These Jurassic deposits may have been followed, over much the same area of deposit, extending south-eastward to the river Murray, by others, in those Cretaceous times when the Angiosperms rapidly dominated the Gymnosperms. This domination may, it has been suggested, have been accelerated by the contemporaneous evolution of the higher honey-sucking and pollen-eating groups of insects, the Lepidoptera and Hymenoptera. Gondwanaland seems to have been dismembered by the sinking of the northern Indian Ocean in Jurassic times, an earth-movement followed, perhaps, by the outpouring of the vast mass of basaltic lavas of the Deccan. Similarly extensive subsidences, such as

those of the Western Mediterranean, the South Atlantic, and the Western Pacific, may have occurred in later, *i.e.* Tertiary times. These, and the fact that Eocene and Oligocene rocks are crumpled up, together with Jurassic and Cretaceous ones, into the great fold-mountain axes of our continents between the more primitive earth-masses, make it difficult to think of any land-distribution much like that of to-day before Miocene times. On the other hand, by the close of the Pliocene period we may have had oceans, continents, and a distribution of the main groups of plants in very much the same proportions as now.

As the cold of the Glacial period came on, it seems to have driven heat-loving or "tropical" plants southward, followed by those of warm-temperate, cold-temperate, and polar latitudes.

"We may suppose that the organisms which now live under latitude 60°, lived during the Pliocene period further north under the Polar Circle, in latitude 66°-67°. Now, if we look at a terrestrial globe, we see under the Polar Circle that there is almost continuous land from western Europe, through Siberia, to eastern America. And this continuity of the circumpolar land, with the consequent freedom under a more favourable climate for intermigration, will account for the supposed uniformity of the sub-arctic and temperate productions of the Old and New Worlds, at a period anterior to the Glacial epoch" (Darwin, *Origin of Species*, p. 333).

As such ferns as *Matonia* and *Dipteris* in the Malay Peninsula are survivals of a still earlier flora, so *Liriodendron* and *Sassafras* in China and the Southern United States are survivals of the Cretaceous flora; and *Ramondia* and *Dioscorea pyrenaïca* Bub., representing the tropical *Gesneraceæ* and the Yam family in the Pyrenees, and *Myrtus communis* L., *Laurus nobilis* L., *Ficus Carica* L., and *Chamærops humilis* L., in the Mediterranean area, are sole survivors of their several orders from pre-Glacial times. Many genera which then flourished in Europe, and still grow in eastern Asia and in eastern North America

"were exterminated during the Glacial period, being cut off from a southern migration, first by the Alps, and then by the Mediterranean; whereas in eastern America and Asia the mountain-chains run in a north and south direction, and there is nothing to prevent the flora from having been preserved by a southern migration into a milder region" (A. R. Wallace, *Island Life*, ed. ii. p. 123).

By ascending to greater altitudes on meridional

mountain-chains, such as the American Cordilleras, the Cameroons, or the Malaysian axis, northern plants may have crossed the torrid zone to descend in the southern hemisphere, and such migrations may have long antedated the Glacial Period. In this way the Scandinavian flora seems to have reached into every latitude, extending, perhaps, by way of a chain of "sub-antarctic" islands to Tasmania and New Zealand. Other important elements in the New Zealand flora seem to have traversed a Miocene land connection from New Guinea.

With the gradual disappearance of Glacial conditions, migration may be presumed to have taken place in reversed directions. As there is every reason to believe that the whole of Scandinavia, of the British Isles, and of Canada were glaciated, the whole of the existing floras of those countries must be the result of such post-Glacial return migrations. As there is evidence that the prolonged Glacial cold was intermitted by milder periods, so it has been argued that it was followed by alternations —at least in north-west Europe—of rainy "insular" periods and drier "continental" ones. During the former, for instance, bog-moss accumulated as peat; during the latter pine forests might spring up on the dried-up bogs. During these mild "insular" periods, favoured by warm ocean currents from equatorial latitudes, the so-called Atlantic flora—an assemblage of plants, of African parentage, unable to withstand such severe winter cold as occurs in the inland regions of temperate continents—seems to have spread from Cameroons or Atlas, by way of the coasts of Portugal or Brittany, to Ireland, Cornwall, or the south-west coast of Norway.

Thus only, in the course of long wanderings to and fro, have the floras of different lands attained to the proportions in which their species now exist. Apparently Cretaceous in origin, they have been added to and reduced, and in many cases modified specifically or varietally by tropical heat and glacial cold, by superabundant moisture, and by drought.

BOOK II

THE FACTORS OF DISTRIBUTION

CHAPTER I

THE CLIMATIC ENVIRONMENT AND THE RESPONSE TO IT

It is difficult to classify and arrange in logical sequence the factors that determine or influence plant-distribution.[1] There can, however, be little doubt that climate is the pre-eminent condition. Though climate has been defined as the average of the weather, or of the physical conditions of the atmosphere, and is often spoken of as if it consisted solely in the temperature, moisture, and movements of the air, meteorologists generally in practice include the treatment of the intensity and other characters of the sun's light. It may be well to emphasise at the outset the fact that in nature the various elements that make up climate and other physical conditions, such as aspect and the temperature or moisture of the soil, are so intimately correlated that it is very difficult to analyse their separate action. In estimating the action of these agencies upon the life of plants, with special reference, so far as we are concerned, to distribution, it has also to be borne in mind, not only that the

[1] "At least six main factors have contributed to the present distribution of organisms, and none of these can be ignored. They may be grouped in pairs: (*a*) the physical peculiarities of the region under discussion, and the constitutional peculiarities of the living creatures; (*b*) the original headquarters of the stock (usually uncertain), and the means of dispersal in each case; (*c*) the physical changes of climate, earth-movements, etc., in the region; and the changes brought about in the struggle for existence between the various living tenants of the country. It may even be permissible to use a mathematical expression and say that the distribution is a function of six factors, some of which are variable dependently and others independently" (Professor J. A. Thomson in *The International Geography*, p. 86).

physiological requirements and response in growth or energy of each species may be different and so require to be differently stated, but also that the life of any plant is made up of an infinite number of phases, each of which may have its separate requirements and limits; the lowest, best, and highest degrees of intensity of light, of temperature, or of moisture, for instance, at which it can take place.

A. Light

Light depends mainly upon latitude, the obliquity of the sun's rays increasing and the intensity of light diminishing, from the equator towards the poles; while the length of the day, *i.e.* the duration of light, increases in proportion. Thus in polar regions the sun daily describes an almost complete circle in the sky, its light falling upon plants from every side in turn, though at a low angle. This is termed "circumpolar light."

Although light varies less within the limits of one latitudinal zone than will heat or moisture, it may be greatly diminished by the shade of trees or other plants, whether all the year round, as in the case of the evergreen forests of the tropical regions, or during the summer, as in the deciduous forests of temperate latitudes. Under these circumstances, also, filtered, as it were, by passing through the overhanging foliage, it will cease in the main to be white light or to consist of rays of various refrangibilities, some rays being absorbed. So, too, in passing through water of any depth some light is reflected, some absorbed, and all refracted; so that submerged plants are much in the position of shade plants.

While the duration of light varies with the season, its intensity increases in the rarefied air of mountain heights, while the presence of moisture in the air, whether invisible or condensed as cloud, also exerts a modifying effect upon light.

Not even in deep sea is it apparently too dark for bacterial life, nor in caves for the development of moulds; but green plants, requiring light for the formation and action of their chlorophyll, are absent from such situations. When light is small in amount plants may apparently develop structures specially adapted

to the convergence of its few rays upon the chloroplasts. Spheroidal transparent cells in the protonema of a moss (*Schizostega*) growing in caves, and the projecting epidermal papillæ causing the velvet-like "pile" on many leaves in dense tropical forests have been thus explained.

Too little light is often fatal to buds and lateral shoots, as when the lower branches of trees are killed off under dense forest canopy. Under such weak illumination flower-buds will often not form; or "cleistogene" flowers, those which do not open, may, as under the leaves of violets in summer, replace those that do.

Light of moderate intensity is favourable to the growth of leaves in area, and is essential for (i.) the formation of chlorophyll and some other pigments; (ii.) photolysis, that decomposition of carbon-dioxide which precedes the formation of formaldehyde; (iii.) some movements; and (iv.) the assimilation of nitrates. For the formation of chlorophyll, yellow or orange light is most effective; and for photolysis the red end of the spectrum is the "optimum," or most favourable, condition; but for the assimilation of nitrates the violet end is the optimum. Some free-swimming Algæ move towards the light, others away from it: most roots curve away from light, or are "negatively heliotropic"; whilst most shoots, on the contrary, are "positively heliotropic," *i.e.* bend towards the light. The chloroplasts near the surfaces of leaves arrange themselves parallel to the leaf-surface, which thereby appears darker green, in diffused light; and at right angles to the surface in direct light, when the leaves appear paler. The former movement is termed *epistrophe;* the latter *apostrophe*.

Light, even when weak, and especially violet light, checks the growth of axial structures in length. The dwarfed, tufted habit of Alpine plants may certainly be correlated with this condition: they are "sun-plants," specially adapted to the intense direct sunlight of cloudless skies and shadeless situations. At the same time, such plants often avoid direct sunlight to some extent by turning their leaves edgewise. They have, as a rule, colourless epidermal cells, the chlorophyll being in the well-developed palisade-tissue or hypoderm. Sun-plants are also characterised by the intense colouring of their numerous flowers. The House-leek, a sun-loving,

tufted plant, when grown in shade, elongates and produces smaller leaves. Shade-plants, on the other hand, have their chlorophyll in the epidermal cells of the leaf, and are commonly few-flowered. These contrasting conditions may occur, according to surroundings, in the structures of the same species.

Very intense light, especially if violet, disintegrates chlorophyll, turning it yellow or brown; and is actually fatal to protoplasm, thus causing the death of many Bacteria and Confervæ. On the other hand, the absence of light produces "etiolation," a lengthening of slender internodes, with small leaves, and the replacement of chlorophyll by the pale yellow etiolin.

The long-continued light of clear northern latitudes, though at a low angle, favours rapidity of development. Thus barley passes through its life-cycle, from sprouting to ripening, more rapidly there than farther south.

The slope of the ground and its aspect, or the point of the compass towards which sloping ground faces, have an important action in determining the time when, and the angle at which, light falls upon plants. Thus it is only on the cliffs of Spitzbergen that many Arctic species receive enough radiant energy from the sun to ripen fruit. Trees commonly come into leaf earlier on the side facing the sun.

B. Heat

Heat is far more influential than light in determining plant-distribution. Its distribution over the earth's surface depends mainly upon latitude, the grouping of seas and land-masses, and altitude. The inclination of the earth's axis towards the plane of the ecliptic produces those differences in the length of day and night which constitute seasons, and divides the earth's surface into latitudinal zones, the Torrid Zone extending for $23\frac{1}{2}°$ on either side of the Equator, the Frigid Zones for $23\frac{1}{2}°$ from either Pole, while the two Temperate Zones (North and South) each occupy the 43° between one of the Tropics and the Arctic or Antarctic Circle. But though these mathematical zones do bound or limit areas according to the total proportion of solar radiation they receive, they are very far from bounding regions having the same climates or even temperatures. Of the sun's rays

received at the upper limits of our own atmosphere, probably little more than half reach the surface of the globe itself, most of those which are absorbed during their passage through the atmosphere being taken up by the dust particles upon which moisture condenses to form cloud. The atmosphere is itself so nearly transparent to the direct rays of the sun that, as is well known, the sun may blister an alpine climber when the air around him is below the freezing-point of water. Much of the direct heat of the sun will be absorbed by the leaves of plants upon which it falls, though not as large a proportion as by the blackened bulb of a thermometer; and it is well to bear in mind that many plants live in the sun, while our records of temperature are mainly taken from instruments kept in shade. The temperature of the air depends upon the amount of the heat reflected from the earth's surface which is absorbed by the moisture in the air. The amount of this reflection differs greatly according as the surface is land or water. Land reflects more of the heat that falls upon it, while the high specific heat of water causes it to render much of its supply of heat latent. The seas, or other bodies of water, are thus more slowly heated than the land, and retain their heat longer, giving it to the air more slowly, and so lowering the general temperature of the air in summer and raising it in winter, and producing in their neighbourhood those equable or "insular" climates with but little difference between summer and winter temperatures, or "hiberno-æstival variation," which contrast with the extreme or "continental" climates in the interiors of continents.

The first step towards a scientific geography of plants was taken when Humboldt, in 1815, proposed to trace over the earth's surface *isotherms*, or lines joining places having the same temperatures. The extent to which these lines fail to run parallel to the parallels of latitude is a measure of the extent to which the distribution of land and water modifies the latitudinal distribution of heat. The isotherm of the mean annual temperature of 82° F. corresponds roughly with the Equator; but the position of monthly isotherms varies with the seasons, *i.e.* with the apparent northward or southward passage of the sun, from being vertical over the Equator at the Equinoxes (Spring and Autumn) to being so over either

Tropic (Summer and Winter). As a mean temperature may be a mean between extremes differing much or little, it is important from the point of view of plant-life to trace the isotherms of greatest heat and greatest cold. It is more usual to take those of the hottest and coldest months (July and January), which are known as *isotheres* and *isocheims*. Whilst in the South Temperate Zone, in which there is a continuous ocean belt, the isotherms are nearly parallel, in the Northern Hemisphere they are generally deflected polewards during the summer as they traverse the continents, and in a reverse direction in winter, or when traversing the ocean. Ocean-currents, conveying large volumes of water, heated in equatorial, or cooled in polar, regions, modify the positions of isotherms.

Most of the water-vapour in the atmosphere being in its lower portion, high ground with drier air radiates heat more than does low ground, and thus has lower air-temperatures. Temperature falls about 1° F. for every 300 feet of altitude. Soils, too, differ both in the amount of heat they reflect, owing to their light or dark colour, and in their retention of heat, according to their moisture and porosity. Dry soils with much interstitial air, such as sand, carry off heat more slowly than damp, close-textured soils, such as clay, and as a consequence both become hotter themselves and maintain a higher air-temperature overhead.

The requirements of a plant as to heat vary, not only according to its species, but for each of the various stages and processes in its life. For each of these, as well as for the existence of the plant, there are three *cardinal points* or degrees of temperature: the minimum or lower critical temperature, or lower zero-point, the optimum, and the maximum, upper critical temperature, or upper zero-point. Nowhere on the earth's surface does the temperature appear to be too low or too high for some plant-life. At Yakutsk, where the temperature falls to − 62° C. (below − 79° F.), 200 species survive, some even hibernating when in flower-bud. Seeds, and other parts of plants containing but small proportions of water, are capable of resisting intense and prolonged cold, the destructive action of cold being apparently either the rupture of tissues by the formation of ice within the cells, or drought. Herbaceous perennials

escape low surface temperatures by their "*geophytic*" habit, *i.e.* by dying down to underground and often deeply-buried structures; whilst annuals, hibernating or "perennating" in the seed stage, are only practically affected by the temperature of the two to six months of their vegetation-period. One of the chief dangers of winter cold to perennials appears to be excessive transpiration when the cold of the soil inhibits the action of their roots.

On the other hand, not only do Diatoms withstand temperatures exceeding 80° C. (176° F.) in the waters of hot springs, and saxicolous lichens 60-70° C. beneath the cloudless summer skies in the desert; but flowering plants, such as *Rhododendron javanicum* Benn., will flourish amid the vapours of volcanic fumaroles; and others, in India, when the shade temperature reaches 50° C. (122° F.), must be themselves heated to 60° or 70° C.

The lowest temperatures at which seeds have been observed to germinate range from below 1° C. for *Medicago sativa* L., 1.8° C. for Flax, and 2° C. for many Alpine species, to over 16° C. for *Theobroma Cacao* L. Wheat will not sprout below 5° C. or above 37° C., while the Vegetable Marrow will sprout at 42° C. The roots of many *Cruciferæ* will absorb water slightly above the freezing-point; but those of the Tobacco not below 12° C. Respiration has been detected in *Juniperus* at −10° C. and photosynthesis at −40° C.; whilst Arctic Algæ produce their reproductive structures in winter when the water is not above −1° C., and may grow to their full lengths when it is but little above 0°. Aquatic plants in general are less exposed to rapid or extreme fluctuations of temperature than are terrestrial species; and, consequently, the minima and maxima of necessary temperatures are nearer together in the case of the former. In many plants of temperate or cold latitudes it has been observed that a low temperature favours the production of floral organs, a higher one that of vegetative shoots.

Whilst only temperatures above a certain minimum and below a certain maximum have any apparent effect on plant-life or its various phases, it is rash to conclude that the plant is not subsequently affected by those outside these limits. Allowance must at least be made,

in considering the effects of Spring sunshine, for heat received by perennial plants in the previous season, and for heat in the soil and its water-content. A little consideration of the methods of the horticulturist will remind us that he not only regulates the supply of heat to the air round his plants at various seasons, but also controls their supply of light, moisture, and bottom-heat.

It appears immaterial, within surprisingly wide limits, whether a plant receives heat in a short or a long period of time. In northern India, for example, Wheat is harvested within three months of being sown; in Palestine within five months; in Sicily in six; in Central Europe in nine; in Yorkshire in eleven, and in Scotland in thirteen. At the same time, the duration of the period when useful temperatures render active plant-life possible produces marked effects upon the physiognomy of vegetation. Annual species are rare in Arctic latitudes and alpine altitudes, because the period in which useful temperatures exist is too short for their life-cycle; whilst our early-flowering perennial herbs depend on the stored-up food and energy of the preceding autumn; and the dense evergreen vegetation of equatorial regions is correlated with an almost complete absence of seasonal change, heat and moisture prevailing throughout the year, and vegetation, in consequence, undergoing no period of rest.

The distributional limits of species seem, however, to be rather determined by the extremes of cold and heat to which they are subjected than by annual mean temperatures. Those that are checked from extending polewards by the want of sufficient heat, such as many annuals, are termed *philotherms*, or heat-lovers; whilst those that are checked by too great cold, such as most evergreens, are known as *frigofuges*, or cold-fearers. Owing to the rarity of frosts in insular climates frigofuges can spread more polewards in them; while philotherms expand more readily in continental regions, often passing through the unfavourable extreme of climate either in the seed stage or as geophytes, *i.e.* underground.

It is difficult to correlate definitely many external characteristics of form in plants with heat; but it seems that the prostrate or "espalier" habit of woody plants just below the snow-line, such as species of Willow, Birch, and Juniper, and the development of rosettes of

fleshy leaves closely pressed upon the ground are adaptations to the economy of heat. The dense covering of hair in the Edelweiss or on many buds, and the persisting dead leaves of arctic and alpine plants, are explained as a non-conducting protection against rapid freezing or thawing and excessive transpiration.

Internally, the same condition seems to determine:

(i.) The secretion of fat instead of starch, and, perhaps, that of resin;

(ii.) The development of the red or purple anthocyan in lieu of chlorophyll in grasses near the snow-line, and in plants in dense shade, transforming light-rays into heat; and

(iii.) The formation of wood, as in alpine undershrubs, or other dry structures, such as those of mosses and lichens, which are better able to resist cold than succulent structures.

What is usually miscalled acclimatisation is merely the introduction of species from climates as nearly identical as possible with that of the land to which they are brought. Very little can apparently be done to acclimatise a plant to a climate other than its own. What does seem possible in this direction is to secure the healthy—if somewhat more rapid—growth of broad-leaved trees in a climate slightly warmer than that to which they are native.

C. Atmospheric Moisture

No active life is possible in the absence of water. It is essential to germination, is itself an important food-material, and acts as a solvent for all the mineral food-materials, and as a vehicle for the absorption and transference throughout the plant of all food-materials and foods. The physiological activity of protoplasm is checked unless it is saturated; that of the entire cell unless it is maintained by such saturation in a state of turgor; and accordingly the opening of the stomata, which permits transpiration, does not take place when the supply of water is absent.

Some cryptogams, such as lichens, some mosses and Selaginellas, and parts of some of the higher plants can, however, remain in a state of suspended vitality when almost completely desiccated.

The importance of water in plant-geography exceeds in some respects that of heat, because its distribution is more irregular. It exists in two main states, either as invisible atmospheric moisture, or precipitated, whether as dew, mist, rain, snow, running or standing waters, or that in the soil. The amount of invisible moisture in the air increases with the temperature; but the condition of atmospheric moisture which is most important with reference to plant-life is the saturation deficit, or the amount of moisture by which the air at any time or place falls short of saturation. This regulates the amount of transpiration or loss of water by the plant.

Moist air is correlated with the same structures in plants as is feeble illumination. Many shade-plants (*dryads* or *sciophytes*) and submerged aquatic plants, which are very similarly conditioned, have long internodes, smaller, thinner, and more transparent leaves, with little palisade-tissue, vascular tissue, or mechanical tissue, but with large intercellular spaces. Sun-plants (*oreads* or *heliophytes*), on the other hand, being adapted to dry air and, therefore, to a desirably limited transpiration, are more compact in growth, with thick leaves, often vertical, and small intercellular spaces in them.

It is true that the greater part of the water taken in by plants is derived by them, not from the invisible moisture of the air, but from precipitated moisture, especially rain, which has entered the soil. Thus it is upon the geographical distribution of rainfall that many of the main features of the earth's vegetation depend. In the immediate neighbourhood of the Equator we have the "zone of constant precipitation," where a very high rainfall is almost equally precipitated throughout the year; and there we have the equatorial evergreen forest-zones of the Amazon and Congo basins, known technically as the "hot rain forest" or *Selva*. Over most of India, Further India, and the coasts of Mexico, a heavy periodical, or "monsoon," rainfall, confined to part of the year, produces the less dense "monsoon forest"; whilst on the higher ground of eastern Brazil, British East Africa, and northern Australia we get a lower rainfall and the lower-growing "hot thorn forest," or *Caatinga*, with many deciduous trees. With a less heavy and less continuous rainfall in tropical latitudes, as in the southern Soudan, Rhodesia,

east-central Australia, Venezuela, and southern Brazil, we have the open, park-like area of tall grasses known as *Savana*. With scanty summer rains in similar latitudes, as in the northern Soudan, Somaliland, Bechuanaland, and central Australia, we get the *Scrub-lands*, especially characterised by spinous, gum-yielding trees and shrubs such as the Acacias; whilst in the practically rainless areas which accompany the perennially high atmospheric pressure and outflowing air along the lines of the Tropics, as in the Sahara, Arabia, Thar, west-central Australia, Kalahari, and Atacama, and in the mountain-girt plateaux in the centre of monsoon areas, as in Gobi, Iran, the Transcaspian region, and the Great Basin of North America, we have *Deserts* in which vegetation is all but confined to oases surrounding springs.

In temperate latitudes also we have grassy *Steppes*, as in Argentina, western New South Wales, northern Persia, south-western Siberia, and the prairie region of the western United States and Canada, where with winter snow we have a small summer rainfall and three types of forest. In the Warm Temperate Zone, from about 30° to 45°, we have evergreen forests; but those of western regions, such as the Mediterranean area, south-west Cape Colony, and south-west Australia, have winter rain, and are characterised by such small, dry leaves as those of the olive; whilst eastern regions, such as China and Japan, the eastern United States, Uruguay, and south-east Australia, have summer rains, the effect of which is seen in the large thick leaves of *Camellia* and *Magnolia*. In the Cold Temperate Zone, between 45° and 60° in Western Europe, and between 45° and 50° in south-eastern Siberia and south-eastern Canada, where summers are warm and wet, we find mixed forests of broad-leaved deciduous trees, followed on the north by the belt of coniferous, needle-leaved evergreens.

From this it is obvious that nearness to the sea, altitude above sea-level, the direction of prevalent moisture-laden winds, and the presence of mountains which will cause them to precipitate their moisture, profoundly modify rainfall, and thus affect the distribution and character of vegetation. It will also be seen that the season at which rain falls is of the greatest significance. The hot, dry summers of the Mediter-

ranean produce more steppe than forest and a type of vegetation adapted to economy of transpiration, whilst the summer rains of east Australia produce a much more luxuriant tree-growth.

The minor distinctions of habitat, or situation, within the great climatic regions are largely determined by the presence of water in the soil. Thus in England Alders and Willows grow in undrained land, Elms will flourish on stiff clays, Oaks prefer a loam as being less liable to stagnation, while Beech requires a warm, well-drained soil. It is not surprising that no external influence has resulted in such marked modifications of plant structure and form as has the greater or less supply of moisture in the air and in the soil, or other medium in which plants grow. This, however, is not a question of the amount of water present, but of the amount available to the plant. Salt water and acid soil-water, such as that in many stagnant bogs, cannot be utilised by the majority of plants; nor will roots absorb water when the soil-temperature falls below a certain point.

Apart from aquatic plants, which we will consider separately, the two most marked types of adaptation in this respect are those of (i.) plants growing under conditions in which an abundant and constant supply of water necessitates increased facilities for its discharge, which are termed *hygrophytes;* and (ii.) those of plants in which a scanty supply has led to the development of means for increasing absorption and diminishing transpiration, which plants are termed *xerophytes*. Plants of intermediate character, not specially modified for excessive moisture or drought, are termed *mesophytes*, among which we may class those plants, like our deciduous broad-leaved trees and shrubs, which develop bud-scales and corky periderm—xerophilous characters—in the cold and dry season of winter, but thin leaves, like those of hygrophytes, in summer. These have been termed *tropophytes*. Hygrophytes may have a poorly developed root-system; long stems, often climbing; large thin leaves with numerous stomata and, sometimes, with long acuminate points or "drip-tips" and other water-pores from which drops of water exude; and no prickles, hairiness, or waxy bloom on the surface, or succulence in texture. This type is abundantly represented in the Amazon forests.

Xerophytes, on the other hand, may have long or copious roots; corms, bulbs, tubers, or other forms of fleshy underground stems, so frequent in the plants of Cape Colony; a dwarfed habit, sometimes leading to the formation of dense, cushion-like masses, as in the Balsam-bogs of the Falkland Islands; or unbranched, barrel-shaped stems, as in Baobabs and some Cacti; branched and fleshy ones, as in *Colletia*, *Opuntia*, and *Phyllocactus ;* or much-branched, whip-like, and nearly leafless forms like our Common Broom. They commonly develop spines and prickles, as is so strikingly characteristic of the Acacias and Euphorbias of Africa and of the *Cactaceæ* which "represent" the latter in America. They commonly secrete resins, gums, and essential oils: resins being markedly characteristic of the *Coniferæ*, gums of the Acacias, and essential oils of the *Labiatæ*, which abound in the Mediterranean region, and of the *Myrtaceæ*, which include the Eucalypti of Australia. Their leaves are generally persistent, thick, with a thick cuticle, and few stomata, which are sunk below the general surface of the leaf. They may be large and succulent, as in the African Aloes and American Agaves; or smaller, as in the fleshy rosettes of the House-leek (*Sempervivum*) and other *Crassulaceæ* and many shore-plants, with a thick water-storing hypoderm; dry and rigid (sclerophyllous), as in Olives, Evergreen Oaks, *Proteaceæ*, and the needle-leaves of the *Coniferæ ;* with inrolled margins, as in Heaths and the grasses of sand-dunes; or delicate in texture but folding automatically when exposed to strong sunlight, as in the compound leaves of *Mimosa* and *Oxalis*. The flowers of xerophytes are sometimes protected by numerous membranous bracts, as in the *Proteaceæ* and "Everlasting-flowers" of Cape Colony; and the whole surface is often densely clothed with hairs or scurf-like scales. Xerophilous vegetation characterises not only deserts and semi-deserts or steppes, but such other situations as porous, sandy, or calcareous soils, saline sea-shores, acid bogs, and the cold soils of sub-arctic and alpine zones.

According to their requirements as to temperature and moisture, plants are divided into five classes:

1. *Hydromegathermic*, in a temperature in which the mean of the coldest month exceeds 16° C. (=about 60° F.): plants known to gardeners as "Stove-plants," now

mainly equatorial, but far more widely distributed in early geological periods.

2. *Xerophilous*, in climates in which no month has twelve days with rain; including the "Succulent plants" of gardens.

3. *Mesothermic*, in a temperature in which the mean of the coldest month is below 16° C., but which does not fall below the freezing-point of water for long together; requiring also, at least during certain periods, abundant moisture: the "Greenhouse plants" of Sub-tropical and Warm Temperate zones which require protection from frost. These were represented within the Arctic Circle in Tertiary times.

4. *Microthermic*, adapted to prolonged periods of frost, requiring little heat, rain, or snow throughout the year, and a period of rest caused by the cold: "Hardy plants" in our climate.

5. *Hekistothermic*, in a temperature in which the mean of no month exceeds 10° C. (50° F.): "Alpine plants" which live beyond the limit of tree-growth. Accustomed to be covered for long periods by snow, they can endure the long "night" of Arctic latitudes, but require protection from the full sunlight and cold drought of an often snowless English winter.

D. Wind

Most plants can readily obtain all the oxygen they require from the surrounding air. The slow diffusion of air in water, especially in stagnant water, is associated with large air-storing spaces and passages in aquatic plants; while many plants growing in mud develop special *aërenchyma*, or air-secreting tissue, mostly of cortical origin, formed of thin-walled cells, and occasionally special respiratory roots, or *pneumatophores*, coated with such *aërenchyma*. The "knees" of the Swamp Cypress (*Taxodium distichum* Rich.) are a striking example.

Wind, that is the air in movement, has great indirect and direct effects upon plant-life and distribution. It is the cause of wave-action, and—when constant in direction—of ocean currents. It greatly modifies the distribution of heat, both in such currents and in that which it carries itself, and also that of atmospheric

moisture and rain. Winds are dependent upon differences of atmospheric pressure; and we recognise seven irregular *belts of climate*, characterised by their winds, and dependent upon the existence of an equatorial belt of heated, moist, upward-tending air and consequent low pressure, flanked by two belts of high pressure in about latitudes 23—35°. Apart from the great local irregularity of the Asiatic monsoons, these belts are:

1. The Equatorial Belt of calms and variable winds and constant precipitation, known nautically as the *Doldrums*, with sultry, often thunderous, humid air and little seasonal variation, extending from 3° to 11° north of the Equator.

2 and 3. The North and South Intermediate or *Trade-Wind* Belts, so called by the Spaniards and Portuguese of the sixteenth century from the utility of the N.E. wind in making the voyage to the West Indies. These areas extend between 3° and 35° north and south of the Equator, and are characterised by the constant N.E. and E. winds in the Northern, and S.E. and E. in the Southern Hemisphere, with dry air and small rainfall, since the wind is constantly moving from colder to warmer latitudes, and cannot pick up moisture fast enough to maintain saturation.

4 and 5. The North and South High-Pressure Belts, the Calms and Variables of Cancer and Capricorn, or *Horse Latitudes*, somewhat poleward from either tropic, with very hot, dry air and strong winds.

6 and 7. The Higher North and South Latitudes, or *Anti-Trades ;* the Northern with "Westerly Variables," or South-westerly wind; the Southern Belt, that of the *Brave West Winds*, N.W. and W., between 40° and 50° S. lat., as regular as the Trade-winds and stronger. The chief rainfall in these belts is associated with the great atmospheric eddies known as *cyclones*, which are most frequent in winter.

The position of these belts changes with the season. The equatorial belt of low pressure always lies nearly under the vertical sun; and, consequently, in the northern summer it swings to the north, and in the southern summer to the south, displacing the tropical high-pressure belts alternately northward and southward. Thus all parts of the earth's surface traversed by this equatorial rain-belt in its annual movement have

a rainy season when it does so, and a dry season during the rest of the year; while near the Equator, where it traverses the region both in its northward and in its southward swing, two wet and two drier seasons can be recognised.

The name *monsoon*, or season, was originally applied to that wide-spreading system of semi-annually reversed circulation which owes its origin to the vast concentration of land in Asia. During the winter, from October to February, when the "continental" temperature of Central Asia falls very low, and the barometer is proportionately high, the north-east or winter monsoon sweeps down over the Himalayas as a dry season, save to the S.W. of the Bay of Bengal. In May the conditions are reversed. High temperature and low pressure begins to prevail in Central Asia. *The* monsoon, as it is called in India, sweeps from the S.W. across the Arabian Sea with heavy rain on the Western Ghats, known as "the bursting of the monsoon." In the Ganges valley it blows along the foot of the Himalayas from the S.E.; and this wet monsoon continues till August. These winds affect the currents of the northern half of the Indian Ocean and the climate of all Asia, Borneo. North-west Australia, and Madagascar. Similar conditions occur on a smaller scale in the Great Basin of the Rocky Mountains, in North Africa, Australia, and the Spanish Peninsula.

Whilst winds may carry oceanic influences inland, as in Western Europe, they may also carry continental influences seaward, as off Eastern Asia.

The drifting of sand by wind, especially on the coast and in the arid areas of the tropics, produces the marked conditions of sand-dunes and deserts, with their characteristic vegetation, while the upward deflection of atmospheric currents produced by mountain-chains causes the precipitation of their moisture on the windward slope, and may markedly raise the temperature at various levels as compared with corresponding levels on the lee side. The high rainfall on the east side of the Andes and of Australia and on the west of the Indian Peninsula are examples of the one, whilst the warm alpine valleys affected by a "föhn," or daily upward wind, illustrate the latter case.

Wind increases rapidly in velocity in proportion to

altitude, and not only modifies the form of trees and shrubs, but also exerts a marked influence in limiting their altitudinal extension. Its action upon plant-life is both direct or mechanical, and indirect or physiological, the latter being the more important. The slope and bending of trees, the killing of their branches when lashed against one another on the windward side, and the curious one-sided branching produced by the killing of these shoots may all be of mechanical origin. The desiccating action of wind, drying the soil, favouring transpiration, and so drying the plant also, is, however, probably the most important action of wind upon vegetation. It will be intensified where the soil is cold, so that the loss of water by transpiration is not readily made up. It is this which is probably the chief cause of the dwarfing (*nanism*) and adpressed or "espalier" habit of many Arctic and Alpine shrubs, and the cushion-like growth of herbaceous species in similar situations. Bud-scales, investing hairs or wooliness, and the retention of dead leaves or parts of leaves, as in many desert grasses which retain the sheath when the blade is withered, are means of checking this excessive transpiration caused by drying winds.

It is plants growing in exposed situations, such as level grass-lands and swamps, and many of our tallest trees, that depend frequently upon wind for the conveyance of their pollen to the female flower; and the "precocious" development of such "anemophilous" or wind-pollinated flowers, *i.e.* their maturation before the leaves are put out, is a well-known adaptation to this end. The case of the Kerguelen Island Cabbage (*Pringlea antiscorbutica* R.Br.), a wind-pollinated member of the order *Cruciferæ*, most of which order are self-pollinating or insect-pollinated plants, inhabiting, as it does, bare island rocks destitute of flying insects, is specially noteworthy. (Fig. 1.)

So, too, it is the plants of exposed situations that depend upon wind for seed dispersal. It is among steppe-plants that we find whole plants uprooted and rolled along by the wind; among tall trees that we chiefly have winged fruits and seeds; though the feathery pappus, or tuft of hairs, occurs alike in the dandelion or thistle of the plains, in the willows (whether dwarf and Alpine or not), and in the epiphytes, such as

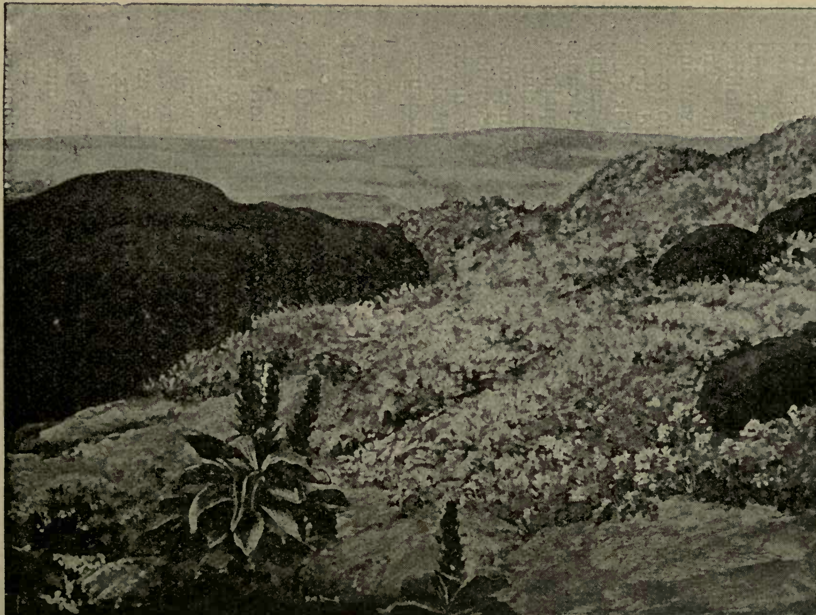

FIG. 1.—View on Kerguelen Island. Kerguelen Cabbage (*Pringlea*) in the foreground. (*From Graebner's "Pflanzengeographie."*)

Tillandsia, on tropical forest-trees. The smallest known seeds are those of some epiphytic orchids, which are so light as to be readily supported even by the gentle upward currents of air in the interior of a forest. The set of powerful winds in one direction must be of importance in the carriage of seeds from the mainland to islands; and there is evidence that small and light fruits and seeds, whether winged or plumed or neither, have been carried upwards of twenty miles in one flight. The minute spores of club-mosses and ferns are still more readily carried in this manner. The flora of oceanic islands, such as Ascension, consists largely of ferns; and no less than eleven species were found on the island of Krakatau three years after it had been covered with lava.

CHAPTER II

THE SOIL

THE nutritive medium in which plants grow is either the bodies of other organisms, in the case of parasites, water, or soil. The conditions of these nutritive media are termed *edaphic* (from ἔδαφος, a foundation); but the science of soils is now often known as *agrology* (from ἀγρός, land). The physical condition, chemical composition, and living inhabitants of the soil are all of the deepest significance with reference to plant-life and distribution, though there is still some difference of opinion as to the relative importance of the first two classes of characters.

THE ORIGIN OF SOILS.—Soils are largely of inorganic or mineral origin; but to some extent organic, the former resulting from the disintegration of rocks. By soil, in fact and in practice, we mean that portion of the land-surface which is sufficiently disintegrated to be penetrated by the roots of plants; and it graduates from the generally looser *surface soil*, which commonly contains some organic matter derived from the decomposition of successive generations of plants and animals, through the more compact and more exclusively inorganic *subsoil* down to the *solid rock*. The disintegration of rock, subsoil, and soil is largely the result of *weathering*,

i.e. the percolation of rain-water, frost, and fluctuating surface-heating; but the roots of plants and burrowing animals, especially earthworms, take an important part in the process so far as the soil is concerned. Soils may, in this way, originate *in situ*, from the disintegration of the underlying rock, when they are termed *local* or *sedentary ;* or they may have been *transported* from their place of origin, as is the case with loess and the blown sands of dunes (*eluvium*), the boulder-clay and gravel of the Glacial Period (*diluvial*), and the brick-earths and gravels of lake and river-basins (*alluvium*).

The Physics of the Soil.—The physical properties of soil, as distinguished from those that are chemical, are chiefly its depth, its texture, including the size of its particles, its "pore-space," density, tenacity, water capacity, capillarity, permeability, and temperature. If the soil be shallow the roots of trees may penetrate it, and their nutrition receive a check on their contact with the more compact and less nutritious subsoil. Shallow soil is also liable to drought, and is, therefore, characterised by xerophytic vegetation. Owing to their greater resistance to weathering, the older, or Palæozoic, formations commonly yield shallower soils than those of more recent geological age.

The size of the particles in a soil may vary very much, the larger ones being known as "stones"; but the density, pore-space, and tenacity of a soil do not depend only upon the fineness of its particles. If these are of uniform size it makes no difference to the volume of the spaces between them whether they be large or small. Particles of the same size, however, may be loosely or compactly arranged so as to have much or little pore-space between them; whilst if smaller particles be intermixed with larger ones, the pore-space may be indefinitely reduced. It has been calculated that with grains one millimetre in diameter there would be approximately 700 grains in a gram of ordinary soil, this number varying inversely as the third power of the diameter of the grains. Thus with a diameter of 0.1 mm. there would be 700,000 grains to the gram. The total area of the surfaces of these particles varies inversely as their diameter, a sphere one inch in diameter having only half the surface of eight spheres of half-inch diameter, though the volumes would be equal. This

extent of surface is important, as it determines the rate at which the particles could be dissolved, the amount of water that can adhere as a film round the soil-particles, and the absorbent capacity of the soil. It has been roughly calculated that a cubic foot of light loam has thus an acre of surface; clay more, and sand less.

Speaking generally, it may be said that the finer the particles of a soil—and consequently the larger the total surface of the particles—the more fertile it is. Ordinary clay contains 400,000 million particles per ounce; land suitable for potato cultivation from 250,000 to 350,000 million; for corn about 280,000, and for onions 350,000 to 450,000 million.

As the pore-spaces are filled either with air or water, the air-content and water-content of a soil necessarily vary inversely. Many physiological processes take place in the soil that depend on the presence of air. Oxygen is required for the germination of seeds, for the respiration of roots; and for the bacteria which manufacture nitrates, whether from free atmospheric nitrogen, or from humus, manure, or other decaying organic matter. Nitrogen is of course also necessary for the former of these last-named processes. About half the pore-space in the soil should, for the healthy nutrition of ordinary plants, be occupied by air; and plants, especially those grown in pots, often suffer from an excess of water.

The water-content, or total amount of water in soil, depends mainly upon rainfall; but the texture of the soil determines its power of retaining water—the slope of the surface influences the rate at which it drains off—and the moisture of the air controls evaporation. The water occurs in the soil under three conditions. It may be (1) free, percolating downwards in porous, coarse-textured soils, so filling the pore-space as to check the respiration of the roots, and thus proving injurious to most plants other than bog-plants. The removal of this free water is the object of drainage.

(2) Capillary water is that which adheres to the soil-particles, especially in fine-grained soils, in films thick enough to move slowly, by capillarity or surface-tension, upwards, or in any direction where the soil is relatively drier. This is the chief part of the water available to the root-hairs of plants.

(3) Hygroscopic water is that which clings to the particles in thinner films so as not to travel by surface-tension, or to be available to the root-hairs, or to be removed until driven off by steam at temperatures above the boiling-point.

Permeability, or the readiness with which free water passes through soils, especially coarse-grained soils, is inversely proportional to capillarity. The retentiveness of soil, *i.e.* its power of retaining liquid, depends mainly on its capillarity; and this again, as we have seen, upon the size of the soil-particles; which practically means the proportion of clay or humus present.

Few, if any, factors are more effective in altering the character of the vegetation of any area than changes in the level to which capillary water rises in the soil—"the water-table," as it is termed.

It is as dilute solutions in the soil-water that plants receive the nitrates, especially of potash, phosphate of lime, sulphates, chiefly of lime, sodium-chloride (common salt) and iron compounds, probably largely carbonate, which they require, together with other less useful mineral substances, such as carbonate and silicate of lime. There is, however, a limit of concentration beyond which roots will not absorb. This seldom exceeds 5 per cent., *i.e.* soil containing water with upwards of 5 per cent. of saline matter is physiologically dry.

Soil temperature is a geographical factor of paramount importance. It depends on the duration and angle of incidence of the sun's heat-rays, the specific heat, colour, porosity, density, and water-content of the soil, the presence of a covering of vegetation, and other causes. The heating power of the sun's rays is proportional to the cosine of the angle of their incidence; so that it diminishes with latitude, and is affected by slope and exposure, or aspect. The specific heat of sand is .2, water being 1; that of peat about .5, *i.e.* it is much easier to heat sand than to heat peat; but dark-coloured soils absorb heat more readily by day, and also radiate more rapidly at night. Porous soils are rapidly heated, but lose heat equally rapidly by radiation, while the conductivity of soils and rocks for heat seems to vary with their density. The great specific heat of water, *i.e.* the large amount of heat required to raise its temperature, makes its abundance in the soil render the soil

cold; but, on the other hand, the water conducts and retains the heat, so that moist soils are warmer in autumn than dry ones. A covering of grass or other vegetation screens the soil from the sun and checks radiation, so that the mean temperature of soil thus covered is lowered, and it experiences less extremes.

Coarse-grained, well-drained soils, retaining little water and thus with a low specific heat, are readily warmed in spring, and are termed early, as opposed to fine-grained, retentive ones.

THE CHEMISTRY OF THE SOIL.—The principal constituents of soils are sand, clay, carbonate of lime, and humus. Sand consists mainly of coarse, incoherent, insoluble grains of quartz, generally coloured by iron-oxides. By itself it forms a light soil, *i.e.* one that offers but little resistance to the plough, and is too unretentive to be fertile.

Clay is hydrated aluminium-silicate, generally coloured by iron; green, blue, or black being due to a silicate, carbonate, or sulphide; yellow or brown to hydroxides. It consists of particles not exceeding $\frac{1}{500}$ of a millimetre ($\frac{1}{5000}$ in.) in diameter, and has great power of retaining water, and if "puddled," or kneaded, when wet, is impermeable and excessively "heavy," *i.e.* tenacious and resistant either to the plough or to root-action. Minute proportions of acids or of certain salts, such as bicarbonate of lime, have the power of coagulating or clotting the clay-particles; and in this condition, which is known as flocculation, it can be readily crumbled. This crumbling takes place when clays are alternately frozen and thawed, as on fallow lands. Mixtures of clay and sand are known as loams. Neither sand nor clay themselves form material of plant food.

Carbonate of lime occurs commonly in rocks as limestone, or, when earthy, chalk; and, in smaller proportions, in other rocks. Mechanically it renders soils lighter in colour, more permeable and friable; but its most important action is probably the neutralising of acids in soils, such as those resulting from the decay of vegetable matter. Clays or sands containing from 5 to 20 per cent. of lime are known as marls.

Humus is the black or dark-brown carbonaceous and nitrogenous substance resulting from the decay of vegetable and animal matter in the soil. Its formation

reaches its maximum where a high rainfall and an impermeable substratum cause the soil to become waterlogged and acid, especially in the absence of lime, the result being peat. Humus absorbs heat, gives soil an open texture, and absorbs and retains moisture.

One ingredient of certain soils must be mentioned here, on account of its marked influence on vegetation. This is sea-salt. Few plants can absorb salt-water, and those that do so are essentially xerophytic in character. Salt in the soil-water, in fact, renders it physiologically dry, so that *halophytes*, as plants of saline situations are termed, are a class of xerophytes. The unfavourable saline condition generally makes a halophytic flora poor in species and in individuals. Among the principal families of halophytes are the *Rhizophoraceæ*, the Mangrove-trees of the tropics (Fig. 2), and the *Chenopodiaceæ*, such as *Atriplex* and the Beets. The most striking external characters of halophytes are reduced, thickened, succulent, glabrous, and often glaucous leaves as in the Yellow Horned-poppy, the Sea-kale, and the Sea-holly. Few others are woody like the Mangroves, and internally we find they have small intercellular spaces, little chlorophyll, and abundant cell-sap. Many species not ordinarily halophytic undergo modification in these directions when growing in saline soil, as, for example, the maritime variety of *Lotus corniculatus* L. *crassifolius* Pers. Others differ in these particulars from related non-maritime forms, as, for example, *Daucus gummifer* Lam., from *D. Carota* L., *Convolvulus Soldanella* L., and *Silene amœna* Huds. On the other hand, halophytes, if transplanted, can grow in ordinary soil. In Asparagus, for instance, almost all the soda-compounds in the wild plant are replaced by potash-salts when it is cultivated in garden ground. Halophytic species frequently occur in the neighbourhood of inland salt-springs.

The Biology of the Soil.—The formation of humus from dead plant-tissues is an important instance of the action of living organisms in the soil, which is not the inert, merely chemical substance it was once thought to be. Aerobic bacteria, micro-organisms, that is, which require free oxygen for their vital action, break down the carbohydrates of plant-tissues, such as cellulose and wood, and their nitrogenous constituents, into "mould" or "mild humus," such as the leaf-mould in woods or

FIG. 2.—Mangrove-swamp near Goa, showing stilt-roots and precocious germination.

the dark powder found in a hollow willow. This is neutral, or alkaline, containing ammonia, but little humic acid. The acid humus of peat-bogs, on the other hand, is the result of the action of anaerobic bacteria, those living in water-logged soil and not requiring free oxygen. Where, however, lime and other bases are abundant, a "mild," *i.e.* alkaline, peat may form, as in the "black soil" of our English fens. This alkalinity may, in fact, be considered as characteristic of "fens," as distinguished from acid "moor" lands.

Earthworms not only swallow and digest large quantities of vegetable matter, as well as the mineral constituents of soil, adding the resultant "casts" as a finely divided humus to the soil, but by their burrowing they admit air into the surface soil. This is important in the life-history of many of the bacteria. These micro-organisms hardly occur beyond a small depth from the surface. Some of them, such as the widely distributed *Azotobacter chroococcum* Beijk., oxidise organic carbohydrate, and thus obtain energy which they employ in "fixing," *i.e.* combining, free atmospheric nitrogen. Others, the *nitroso-* and *nitro-*bacteria, transform respectively ammonia-compounds in the soil into nitrites; and nitrites into nitrates, which can be utilised by the roots of the higher plants. Others again, mostly anaerobic, are *denitrifying*, reducing, that is, nitrates into nitrites, ammonia or gaseous nitrogen. Yet another type, such as *Pseudomonas radicicola* Moore, lives upon waste root-tissue in nodular swellings on the roots of *Leguminosæ* and some other plants, and fixes atmospheric nitrogen as nitrate which is available for the use of the higher plant.

In the humus of dark woods or on sandy heaths, soils, that is, deficient in nitrates, the roots of many of our forest-trees, both broad-leaved, like the Beech, and coniferous, those of the brown saprophytes growing beneath their shade, such as *Monotropa* and the Bird's-nest Orchis, and those of Heaths and other xerophytic plants, are invested with a felt of fungal mycelial threads. These *mycorhizæ*, as they are termed, belong to various groups of fungi: they frequently replace the root-hairs of the plant; and they may, or may not, penetrate the surface of the root which they invest. Not only has their presence been proved to be beneficial

to the plant, but it appears that difficulties in cultivating certain orchids and other plants are very probably due to the absence of the suitable mycorhizæ. They seem to assist the plant to utilise carbonaceous matter in the humus, and perhaps also—at least in some cases—to fix atmospheric nitrogen. *Pinus montana* Duroi has both mycorhizæ and root-tubercles; and not only is it said to fix free nitrogen, but also to benefit the growth of the Spruce when, as in Jutland, the two species are associated.

RESPONSE OF VEGETATION TO SOIL.—The general response of the vegetation to soil-conditions forms the main subject of ecology, and is dealt with later; but we must here notice some cases where it can apparently be definitely assigned to some of the factors that we have just been considering. The incoherent, non-retentive character of sand is reflected in the deep roots, long branched rhizomes, and inrolled leaves of the dune grasses and sedges, such as *Ammophila arenaria* Link, *Elymus arenarius* L., and *Carex arenaria* L., typical xerophytes, though specially separated as psammophytes or sand-plants, or *psammophilous* (sand-loving) plants. Some species common on sands are so because of their *calciphobe* or *calcifuge* (lime-fearing or lime-avoiding) character. Among these are the Spanish Chestnut (*Castanea sativa* Mill.), the Cluster Pine (*Pinus maritima* Lam.), the Foxglove (*Digitalis purpurea* L.), the Broom (*Sarothamnus scoparius* Wim.), Gorses, Heaths, Sundews, and Bracken. Though all these species may be termed *silicicolous*, or silica-inhabiting, considering the insoluble and physiologically useless character of silica, it must be the physical character of sandy soil, rather than any chemical constituent that can act as a positive attraction.

Lime, though in these last-mentioned instances a negative attraction, *i.e.* a repellent, is in a small proportion essential to all flowering plants. Some species flourish on soils rich in calcium-carbonate, *e.g. Anthyllis Vulneraria* L., and *Ophrys muscifera* Huds., the Fly Orchis. Others restricted to calcareous soil in one district, may appear calciphobe or indifferent in another; while that lime-needing plants are not merely those that prefer dry situations is shown by such species as *Phyteuma orbiculare* L., which will flourish in the driest

or most swampy situation if lime is present. Here it would seem as if competition plays an important part. Closely related species often differ markedly in their requirements as to the chemical composition of the soil; but such differences may not be apparent unless the species occur together so as to compete. Thus the Milfoil (*Achillea Millefolium* L.) seems always indifferent as regards much or little lime; *A. moschata* Jacq. will grow, either alone or with *A. Millefolium*, on calcareous soil, but not if *A. atrata* L. is present; whilst, on the other hand, *A. atrata*, indifferent when alone or with *A. Millefolium*, cannot grow on siliceous soil if *A. moschata* be present. In other words, *A. moschata* is relatively less calciphile than *A. atrata*.

Undoubtedly the importance of lime as determining the composition of the flora of any habitat may be due to its neutralising the acidity of the soil, or to its influencing in this way the growth of certain soil-bacteria or mycorhizæ.

The action upon plant-form of a substance in the soil-water usually inert is strikingly exemplified in the case of *Viola calaminaria* Lej., a markedly modified form of *V. lutea* Huds., confined to the neighbourhood of the zinc mines of Aix-la-Chapelle, and yielding a notable proportion of zinc in its ash.

Slow Changes in Edaphic Conditions.—The edaphic conditions of a locality may undergo a cycle of extreme change without any change of climate or geological change of level. Thus a pond containing submerged aquatics, such as *Chara* and *Myriophyllum*, may become overgrown by what is termed the "Limnæa" formation, rooting in the muddy bottom with leaves floating on the surface, such as the Batrachian *Ranunculi*, *Nuphar*, and *Potamogeton*. These may in turn be ousted by reeds, such as *Scirpus lacustris* L. and *Phragmites*, or by such semi-aquatic marsh-plants as the Bog-bean (*Menyanthes trifoliata* L.), the Flowering Rush (*Butomus umbellatus* L.), the Œnanthes, *Acorus Calamus* L., and *Iris Pseudacorus* L. These may in turn give place either to Sedges followed by meadow-grasses, or to *Sphagnum*, followed in time by Ling, Birch, and Pine. Ground which has thus become pine-forest from being covered by water, in which, of course, the water-level has become greatly lower, may conversely pass once

more back to marsh. If the streams that drain it are obstructed by sand-dunes, by trees which may be blown down, or by beaver-dams, their running waters, now stagnant, may be invaded by *Sphagnum*, more trees will be undermined by the displaced water, and the water-level being thus once more raised, forest will become marsh or even lake.

It is suggested that alternating floras attributed to alternating wet and dry climatic periods following the Glacial Epoch may find their true explanation in such a sequence of events, which is, it will be seen, entirely independent of climate.

CHAPTER III

ORGANIC ENVIRONMENT

NEITHER the inorganic (climatic and edaphic) conditions nor the vegetation that responds to them are stable. Constant slight changes, with occasional violent changes, are the order of nature. Thus the balance between plants and their inorganic surroundings and between one species of plant and another is being constantly disturbed, so as to require readjustment. Even when the surrounding conditions are temporarily stable, plants, whether of the same or of different species, are competing for water, food, and light. The growth of a plant in any one spot depends, not only on whether the climate and soil are suitable, but also upon whether the ground is preoccupied, whether the roots of surrounding plants spreading through the soil are draining it of moisture, or the shade of their overhanging leaves is excluding the sunlight.

The dependence of plants growing together (*symbionts*) varies greatly in degree. The benefits of the association may be all on one side, as in most parasites, epiphytes, and saprophytes; or there may be mutual advantages, or the species may merely grow side by side competing on more or less equal terms. Completely parasitic plants, such as Dodders and Broom-rapes, obviously in no way benefit their "host" plants. They are able to dispense with the formation of chlorophyll, or even of

leaves, but have generally to produce an exceptional amount of seed, owing to the risk it runs of not reaching a suitable spot for germination. They vary as to the number of different hosts upon which they are capable of growing; but obviously their distribution depends upon that of the hosts. This is, to a less extent, the case with such partial or "facultative" parasites as the Cow-wheats (*Melampyrum*).

In epiphytes, such as the Algæ, Lichens, and Mosses that grow on the trees of temperate latitudes, and the Orchids, Aroids, Bromeliads, Peppers, etc., on those of the tropics, as there is no physiological attachment to the host plant, there is less restriction as to what species it shall be. This mode of life produces, however, marked structural characters, such as the green aerial roots, sometimes covered with a *velamen* or water-absorbing tissue, the water-holding pitchers of *Dischidia*, and the humus-collecting "pocket-leaves" of the Elks-horn Fern (*Platycerium alcicorne* Desv.). A similar relation to the plants upon which they occur is that of the marvellous rope-like "lianes" of the tropical forests. Belonging to a number of different orders, such as *Ampelidaceæ*, *Apocynaceæ*, *Asclepiadaceæ*, *Bignoniaceæ*, *Dioscoreaceæ*, etc., they agree generally in the long inter-nodes of shade-plants, in their long-stalked and often cordate leaves. They differ from true epiphytes in being rooted in the ground.

The brown *saprophytic* flowering plants, whether dicotyledonous, like *Monotropa*, or monocotyledonous, like *Neottia*, with their reduced roots, leaves, and vascular systems, are but slightly dependent on the trees amongst whose dead leaves they grow, and neither benefit nor harm them. It is, however, interesting to note the unexplained fact that *Monotropa Hypopitys* L. is pubescent when growing under conifers, smooth when under broad-leaved trees.

Commensalism.—Plants of normal nutrition, with normal root-systems and green leaves, merely growing side by side, and having, therefore, apparently similar requirements as to climate and soil, are termed *commensals* (table-companions); and obviously the keenest physiological competition will be between such plants when they are "like," *i.e.* of the same or closely-related species. These "social" plants, as they are termed,

such as the Pines of northern Europe and America, Heather, meadow-grasses, etc., seldom consist exclusively of one species, but one species is often markedly dominant. Such plants are mostly perennial, reproducing themselves largely by such vegetative methods as long, slender rhizomes or stolons, as in the Coltsfoot (*Tussilago Farfara* L.), Butter-bur (*Petasites hybridus* Gärt.), and Marram-grass (*Ammophila arenaria* Link). Many of them are shade-enduring, such as the Woodruff (*Asperula odorata* L.) and most Ferns, whilst others, such as the Beech, have the power of suppressing other species by their own shade.

Whilst it is difficult to exaggerate the intensity of that struggle for existence by which the vast majority of the spores, seeds, and seedlings produced are exterminated, it must be remembered that there are cases of association or commensalism that cannot be considered competitive. In the sparse or "open" vegetation of saltings, and many stretches of barren sand or acid bog, the scattered plants of the few species that can live under such conditions are far apart, and cannot be said to compete. Or, again, two plants living side by side, such as the carpet of moss in a pine-forest, may even be advantageous to one another. The moss protects the soil from desiccation whilst it benefits by the shade of the Pine. Such associations are termed *complementary*. Another case is where species live at different depths in the soil, growing to the surface at different seasons. A common example of this *seasonally complementary* association is that of *Holcus mollis* L., growing near the surface of sandy soil, with the rhizomes of Bracken (*Pteris aquilina* L.) deeper down, and the bulbs of the Wild Hyacinth (*Endymion non-scriptum* Garcke) yet deeper. (Fig. 3.)

New Ground.—The beginnings of competition are seen in the successive occupation of newly-formed open ground. Shore-deposits, whether sandy or clayey, mud-banks in river estuaries, abandoned river-beds, moraine-heaps pushed forward by a glacier, the constantly slipping talus or "screes" on a mountain side, the freshly cooled lava-flows or accumulated "tuff" or ash of a volcano, ground laid bare by a forest or prairie fire, heath ground that has been cleared and pared, whether for fuel or in preparation for cultivation, or the sites of demolished buildings, are examples of such new ground.

The character of the vegetation that will occupy such ground depends partly on the chance of the first comer, partly on the various means of dispersal and multiplication possessed by plants, partly on soil-conditions, and

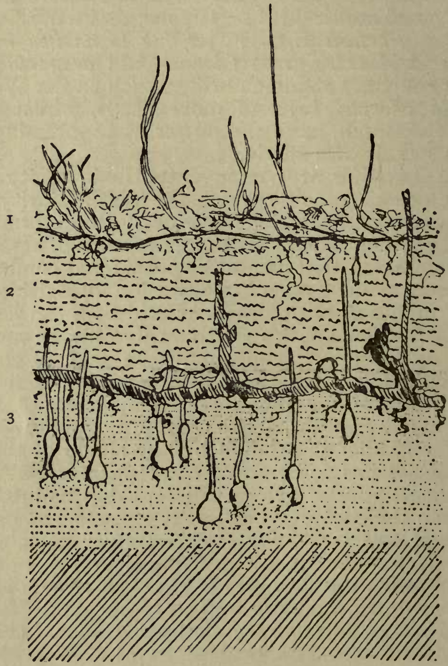

FIG. 3.—Vertical Zonation or Complementary Society of (1) Yorkshire Fog (*Holcus*), (2) Bracken, and (3) Bluebells.

(*By Dr. T. W. Woodhead.*)

then ultimately on competition. Obviously, the first comer is likely to be some neighbouring species.

SUCCESSION.—On the occasionally inundated and salt-saturated deposits of the shore, Algæ will be followed by such halophytes as *Salicornia*, *Salsola*, Crab-weed (*Obione portulacoides* Moquin), and other *Chenopodiaceæ*,

scattered in "open formation," which serve to arrest the mud, and may give rise to little hillocks or *touradons*, on which grow species of *Limonium*, *Statice*, *Plantago*, etc. Here, or where wind accumulates dunes, less halophytic species may establish themselves. Marram-grass (*Ammophila*) will fix the blown sand, a scrub of such species as the Sea-buckthorn (*Hippophaë Rhamnoides* L.) may spring up on the lee of the dunes, and such a sandy flat may be colonised by Pines or Heaths.

On loose, stony, over-drained mountain screes, saxicolous Lichens and Mosses are followed by xerophytic grasses, such as Sheep's Fescue (*Festuca ovina* L.), and these by successively deeper-rooted and taller-growing perennial species, such as Marjoram (*Origanum*), *Ononis*, Juniper, Rowan, and Beech.

Similarly, Algæ and Lichens begin the decomposition of the surface of lavas, to be followed by Mosses and (such rocks being generally porous) xerophytes. Of the striking colonisation of Krakatau, a volcanic island at a distance from the mainland, we shall be speaking in the next chapter.

On the light soil of cleared or pared heath-land, Reindeer-Moss (*Cladonia rangiferina*) and *Polytrichum* may be followed by scattered plants of *Radiola*, before *Calluna* and *Erica cinerea* L. regain their foothold, with Bracken; while later Birch and Pine seedlings are able to colonise. Where, however, the ground has been cleared by fire, certain species are peculiarly adapted to obtain the first place. Such are *Funaria hygrometrica* Sibt., *Senecio sylvaticus* L., *Populus tremula* L., and *Epilobium angustifolium* L. The last-named species is known as "fire-weed" in America, and as "ildmarke" in Denmark.

In these successions three stages are recognised: the *initial*, when the species are few and the plants are in open formation; the *intermediate*, in which the number of species reaches its maximum; and the *ultimate*, in which as a result of struggle, a reduced number of species become dominant in close formation. In the first stages the "pioneers," or first comers, will be so owing to their "mobility," or powers of seed-production and dispersal, and nearness at hand. The small-spored Algæ, Lichens, and Fungi will, therefore, generally come first, followed by pappus-bearing *Compositæ*, such as *Senecio*, small-

seeded Grasses, and "weeds," or "ruderal" (roadside) plants, which are generally characterised by their profuse seed-production. Annuals and biennials will spring up first, but in the intermediate stage will often be mastered by perennials. Wind-disseminated (*anemochoric*) trees, such as Birch, Aspen, and Pine, will perhaps generally precede berry-bearing, bird-disseminated species; while shrubs will obviously be able to grow up sooner than trees. Light-demanding trees will always precede shade-enduring species. The longevity of trees, the fatal effects of their shade upon many low-growing species, and the long periods during which their seeds in many cases retain their power of germination, all tend to give the tree-form the advantage in the ultimate stage of the successions.

The Animal Environment.—The distribution of plants is influenced by animals chiefly in two ways, viz. the dependence of many species of plants upon insects, and even upon special kinds of insects, for their pollination; and the dispersal of spores and seeds by birds and other groups of animals.

While many herbaceous plants in all latitudes are insect-pollinated, or *entomophilous*, it is noticeable that, among trees, it is chiefly in the tropics and warmer temperate zones that we have species with the gaily-coloured, sweet-scented, honey-yielding flowers that are indicative of this characteristic. Most of the trees of colder latitudes are catkin-bearers or conifers, with the precocious - flowering, pendulous, greenish blossoms, extruded stamens, feathery stigmas, and abundant pollen distinctive of wind-pollinated, or *anemophilous*, plants. It is also significant that in many small, wind-swept, oceanic islands flying insects are few or absent, and groups of plants elsewhere entomophilous are pollinated by wind. A striking instance is the cruciferous Kerguelen Island Cabbage (*Pringlea antiscorbutica* R. Br.) (Fig. 1), which is confined to the island from which it takes its name, the Prince Edward and the Macdonald groups.

The absolute dependence of *Yucca filamentosa* L. for pollination upon one moth, *Pronuba yuccasella*, or of *Aconitum* upon *Bombus*, is exceptional, while the similar limitation in the case of the Vanilla orchid proved a check to its cultivation in countries to which it

was not native, until recourse was had to artificial impregnation.

The dissemination of plants by animal agency belongs to our next chapter.

MAN AS INFLUENCING VEGETATION.—No one agency probably has so profoundly modified the distribution of plants as has man. The clearing of forest, whether with a view to agriculture or for timber, the careful removal of "weeds," drainage, the tillage, marling, and manuring of the land, and the introduction of animals foreign to the various countries, have for ages altered the natural balance of species, and have even altered climate. It has been stated that the mean annual temperature of England has probably been raised 2° F. by drainage; and this increase of temperature has of course been accompanied by a much lessened humidity of the atmosphere.

By intentional introduction of new species we have in Britain considerable areas covered with Pine and Larch; the extensive fields in Prussia occupied by the American Potato; millions probably of human beings in Africa mainly dependent for their food upon the equally American Maize; and vast areas in America and Australia occupied by Wheat, Rice, and other Old World species.

Even more striking are the effects of man's unintentional introductions. *Xanthium spinosum* L., a Russian Composite, is said to have been introduced into Wallachia in 1828 in the manes and tails of Cossack horses. Similarly it spread, with cattle and sheep, into Hungary and Bavaria, and, reaching South Africa, proved so detrimental to the wool as to necessitate strenuous laws for its extirpation. The Milk Thistle (*Silybum Marianum* Gaertn.) and the Cardoon (*Cynara Carduncula* L.) have spread over hundreds of square miles of the Argentine Pampas; and these are but some striking instances out of many. It should, however, be noted that many plants introduced to the neighbourhood of docks in ballast, to that of cloth-factories by the combing of foreign wool, or to the site of international exhibitions in the straw of packing-cases, do not survive many years or succeed in establishing themselves.

Many widespread weeds are self-pollinating, small-seeded species; and in the case of such plants, at least,

a single accidental introduction may suffice to establish a species. *Lepidium Draba* L., for instance, is said to owe its prevalence in the Isle of Thanet to the Walcheren expedition of 1809, a farmer having used as manure the stuffing from mattresses on which our fever-stricken soldiers were brought home, and seeds of this species being in it.

CHAPTER IV

DISPERSAL AND MIGRATION

It is obviously advantageous to the species that offspring should be removed to some distance from the parent plant, so as to have at least a chance of occupying new ground free from parental competition, whether of root or shade. The power which a species has of thus getting away from its centre of origin is termed its *mobility*. It depends partly on the number of the spores, seeds, or other detached parts produced, and partly on the special mechanisms and the agencies by which they are dispersed. In a few cases the entire plant is carried from place to place. More often it is some vegetative organ, such as detached bulbils, tubers, offsets, and most frequently it is a reproductive structure, such as spore, fruit, or seed, that is transported.

The "wind-witches" or "steppe-witches" of the centre of the Old World and the "tumble-weeds" of America are sometimes whole plants whose tap-roots are pulled out of the loose soil in which they grow by the bending of the drying stems that bear the ripe fruit. The plant is then rolled as a ball before the wind, many often becoming entangled together in a large mass, and over level plains they may thus travel great distances. The seeds may be shaken out of the fruits *en route*, or, in some cases, these latter only open when moisture is reached.

The little offsets of *Sempervivum* on mountain-ledges become detached, and roll down, or are blown from ledge to ledge, taking root where they rest; the tubers of the Lesser Celandine (*Ranunculus Ficaria* L.) are washed away by runnels of rain-water; while small rounded branches of some Cacti, having barbed leaf-

spines, attach themselves as burs to passing animals and may thus be transported to a distance before rooting.

The Frog-bit (*Hydrocharis Morsus-ranæ* L.) lives mostly in stagnant water, but winter-buds detach themselves from its slender submerged branches, and may rise to the surface and develop into new plants at some small distance. The Water-soldier (*Stratiotes Aloides* L.), the Bladderworts (*Utricularia*), and the Pond-weeds (*Potamogeton*) multiply by similar methods. The subterranean migration of tubers, bulbs, and rhizomes, as, for example, in the Lily-of-the-valley, is in general very slow, although sometimes facilitated by the contractility of horizontal roots. The Butter-bur (*Petasites hybridus* Gărt.), however, will form rhizomatous shoots 1½ metres in length in a single season. The rapid spread of Strawberry plants over the surface of the ground by means of their runners is another familiar example of vegetative migration.

The adaptations for dispersal in spores, fruits, and seeds are, perhaps, for our present purpose, best considered under four groups, dependent on the agency of dispersal rather than on the structural nature of the dispersal mechanism, since in each group we find a very great variety of structures modified to perform similar functions. These four main groups have been termed *bolochores* or sling-fruits; *hydrochores*, plants dispersed by water; *anemochores*, those dispersed by wind; and *zoochores*, those dispersed by animal agency.

The extreme lightness of the minute spores of many Fungi, Mosses, Club-mosses, and Ferns; of the seeds of many Orchids, especially those that are epiphytic; of many parasites, saprophytes, and other plants, will facilitate their dispersal, whether by propulsive mechanism, wind, or water. The seeds of *Goodyera repens* Ait., for example, weigh two-millionths of a gram.

Bolochores.—The bursting of puff-balls as they dry, and the scattering of moss-spores between the teeth of the peristome as the capsule sways in the wind, are analogous, among cryptogams, to the bursting of the drying pods of Broom and Gorse, and to the "censer-action" by which the wind, swaying the dried stalks, shakes seeds between the teeth of the fruit of a Pink, or through the pores of a Poppy-head. The mere drying-up of the tissue of the carpels, causing them to

split apart as in many *Caryophyllaceæ*, *Primulaceæ*, *Delphinium*, *Viola*, etc., is, perhaps, the least specialised type of sling-fruits. Somewhat more elaborate are the cases of the pods of many *Leguminosæ* and the valves of the short fruits of such *Euphorbiaceæ* as *Hura*, *Hevea*, *Mercurialis*, *Ricinus*, etc., in which diagonal contraction produces spiral torsion, often throwing the seeds to a considerable distance. Resilience, or elastic spring, in dry fruit-stalks, and hygroscopic action, like that which ruptures the sporangia of Ferns, aid in dispersal in such cases as many of the *Compositæ*, the Geraniums, and the "hopping" awned grasses. In *Centaurea*, for example, there is an erect, rigid, resilient peduncle, common receptacle which by drying may detach its numerous fruitlets at their bases; dry, hygroscopic bract-scales highly polished on their inner surfaces, and a shuttlecock-like pappus of bristles to each fruitlet. In dry air censer-action jerks the loose fruitlets over the polished curve of the expanded involucre, the pappus-bristles serving, as do the feathers of a shuttlecock, to determine the direction in which each fruitlet shall fall. The curling upwards or away from the central axis or carpophore of the awn or stylar appendage to each of the five carpels in *Geranium* seems also largely hygroscopic; as certainly are the curious jerkings, crossings and uncrossings of the dry awned glumes of such grasses as the Barren Oat (*Avena sterilis* L.). Equally striking are such cases as the Squirting Cucumber (*Ecballium Elaterium* A. Rich.) and the Balsams (*Impatiens*), in which some tissue of the fruit becomes so turgescent with watery sap as to burst the fruit from its stalk, or to separate the carpels, hurling the contained seeds to a distance. The rapid spread of exotic species of *Impatiens* and of *Oxalis* (in which one of the seedcoats becomes turgescent, splits and turns inside out) demonstrates the value to the plant of such dispersive mechanisms.

Hydrochores.—The carpels of the Stonecrop (*Sedum acre* L.) remain closed in dry weather; but when a drop of rain falls into the basin-shaped hollow at the top of the fruit they open, and the small seeds are carried over steep rock-surfaces by trickling runnels. The two most important adaptations to water transport are, however, (i.) the imprisonment of air in structures surrounding

the seed, as in the Water-lilies (*Castalia*), in which genus it is between the aril and the testa, and in the Coco-nut, in which it is between the fibres of the mesocarp; and (ii.) the power of resisting the action of sea-water. A berry-bearing plant of *Asparagus* has been observed to float for eighty-five days, and its seeds have withstood immersion in sea-water for more than a year; while tropical seeds not uncommonly sprout on the north-western coasts of Europe after drifting across the Atlantic.[1]

No adaptations can be more unmistakably efficacious than the waxy epicarp, fibrous air-containing mesocarp, and dense, impervious endocarp of the Coco-nut (*Cocos nucifera* L.) and such similar plants as the Double Coco-nut of the Seychelles (*Lodoïcea Sechellarum* Labill.) and *Nipa fruticans* Thunb. The last mentioned, the smallest of the three, is common in the brackish Sunderbunds, floating for many miles in the waters of the Ganges and the Bay of Bengal without losing the power of germination, as its fossil ally *Nipadites* seems to have done in the tropical British seas of the Eocene period. *Lodoïcea* was known as "coco-de-mer" in the Indian Ocean before it had been found growing, while the Coco-nut is almost universal on tropical shores.

ANEMOCHORES.—Extreme lightness, whether of almost the entire plant; of a head of fruits, as in *Trifolium subterraneum* L. and allied species, the blue-green grass *Spinifex squarrosus* L. on Asiatic shores, and many of the wind-witches of the interior of that continent; or of single fruits, like those of some of the steppe *Umbelliferæ*, or the inflated pods of the Bladder Senna (*Colutea arborescens* L.), is an important adaptation to wind-carriage. Pods of *Leguminosæ*, usually many-seeded, gain lightness in some cases by becoming only one-seeded.

The very varied structural origin of the many wings and plumes or "parachutes" on fruits and seeds is remarkable, the former being specially characteristic of trees and of plants which by climbing attain to situations exposed to wind. It is also noteworthy that the wings

[1] Thus seeds of *Ipomœa grandiflora*, a tropical strand-plant collected in 1888, and placed for a year in sea-water, germinated at Kew in 1891; and seeds of *Entada* did so after floating from the West Indies to the Azores, a distance of 3000 miles.

have very often a spiral twist, and that the seed is commonly excentric, so that the whole structure rotates like a screw-propeller as it falls from the tree, and is the more readily carried horizontally—*i.e.* away from the shade of its parent—by the slightest breeze. It may also be noted that these anemochoric structures occur in a great number of quite unrelated Natural Orders. This is true also of each class of dispersive adaptations.

That most normal dispersive adaptations are merely fitted to carry plants a small distance at a time is exemplified by the Thistles, in which the relatively heavy, well-filled grain—a one-seeded fruit—readily detaches itself from the ring of pappus-hairs, thus commonly dropping to earth but a few yards from the parent plant. At the same time the action of ocean-currents, floating ice carrying earth, tornadoes, or strong persistent winds, must not be ignored.

Zoochores.—Adaptations to dispersal by animal agency fall mostly into two classes: *burs*, or hooked structures, which become entangled in the hair of passing animals; and *succulence*, often accompanied by bright colour, which attracts birds. No burs occur on aquatic plants, or on those over four feet in height, these being obviously out of the way of hairy animals. The hooks which originate in a loop in the style of our common roadside species *Geum urbanum* L., and the twelve or more ferocious harpoons with recurved hooks on the Grapple-plant of South Africa (*Harpagophytum procumbens* DC.), which is said sometimes to prove fatal to the lion, are only two among many varied and complex mechanisms.

Seed-eating birds have muscular gizzards, so that most seeds swallowed by them are destroyed; but fruit-eating species swallow seeds whole, and the testa serves to protect them from the action of the gastric juices. To a less extent the similar swallowing of seeds, which are afterwards ejected uninjured, is carried out by other animals, as, for example, the eating of crab-apples by deer, and the introduction of grasses into new areas by locusts. Even more curious are the established cases of animal-dispersal by mistake, as when ants carry the seeds of the Cow-wheat (*Melampyrum*) to the fine tilth of the ant-hill, mistaking them for cocoons, and when

apparently such beetle-like seeds as those of *Ricinus* are carried to some distance by birds.

Occasional Dispersal.—If, however, these usual methods of dispersal commonly effect small steps in migration, there are rarer possibilities that are not so limited. Even so large a fruit as an acorn is carried by rooks to a considerable distance, and the great pigeons of the Moluccas swallow whole nutmegs and have transported them from island to island. Migratory birds, or birds blown out of their course by strong winds, cover great distances, *e.g.* from North America to Bermuda; or from Europe and Africa to Madeira, and sometimes carry seeds either in their crops, or in pellets of mud adhering to their feet. Freshwater fish swallow seeds, and these might therefore be dispersed by fish-eating birds. Whole plants, even large trees, are often carried down by rivers, and may drift across considerable stretches of ocean bearing their ripe but unopened fruits and, perhaps, also epiphytes, or with seed-containing soil clinging to their roots (Fig. 4). In this case, and in that of icebergs, which have commonly a considerable load of earth, there need be no special structural adaptation of fruit or seed to facilitate their dispersal.

Ecesis.—It is quite possible that one exceptional introduction may lead to the establishment of a species in a new area. Nevertheless, it is important to bear in mind the fact that mere migration need not secure such establishment. The climate and soil must be suitable, and the new-comer may have to hold its own in competition with species already "in possession." For this establishment the term *ecesis* has been proposed.

Those plants which are believed to have reached any district without human action are termed *native* or *indigenous*, but a species known only in one area is termed *endemic*. Such a species may have originated where it is now found, or it may have originated elsewhere, having once had a wider area of distribution, of which its present limited area is the only remainder.

Aliens.—Besides the intentionally-introduced species cultivated by man, whether for food, timber, fibre, medicine, or other purposes, several grades have been recognised among those unintentionally introduced, or *alien* species, according to their degree of ecesis or establishment. Temporary introductions, such as many

brought in ships' ballast, in the straw of packing-cases, or in foreign wool or hay, or escaping from gardens, but unable to hold their own, are known as *casuals*. Many of these may, of course, be repeatedly re-introduced. Weeds of cultivated ground, many of which may be of ancient introduction, though showing their foreign origin by not passing beyond the limits of cultivation and, perhaps, by imperfect adaptation to the climate, are termed *colonists*. Such are our Poppies, Corn-marigold (*Chrysanthemum segetum* L.), Corn-crowfoot (*Ranunculus arvensis* L.), etc., species remarkable for the profusion of their seed-production. *Veronica Buxbaumii* Tenore, first recorded in Britain in 1829, may be termed a colonist. On the other hand, apparent escapes from cultivation that have so far established themselves, or become naturalised, as to be able to spread away from cultivation like native species, reproducing themselves freely, are known as *denizens*. Among British examples we may mention *Chelidonium majus* L., *Myrrhis odorata* L., and the American *Impatiens biflora* Walt., first recorded in Surrey in 1822; *Elodea canadensis* Michx., dating from about 1842; *Claytonia perfoliata* Donn, of somewhat earlier date; *Galinsoga parviflora* Cav., which apparently escaped from Kew Gardens about 1850; and *Mimulus Langsdorfii* Donn.

KRAKATAU.—The relative importance of the different agents of plant-dispersal has been interestingly illustrated in the re-stocking of the volcanic island of Krakatau after its devastation by the eruption of 1883. Other islands are from twelve to twenty-three miles distant, strong monsoon winds blow from opposite directions, and the ocean-currents are not constant in direction. Within three years many wind-carried species of blue-green Algæ, Diatoms, and Bacteria had established themselves on the pumice and ash of the mountain-slopes, and Ferns, with their light spores, preponderated among the larger plants, far outstripping the sea-borne strand-plants. Ten years later various Grasses, *Cyperaceæ*, and Orchids had been added to the list of wind-borne species, which constituted 16-30 per cent. of the whole number of Phanerogams; and 16 species of Ferns were recorded; while fully 39 per cent. of the flowering-plants were sea-borne species. Large piles of floating trees, stems, branches, and Bamboos were met with on the

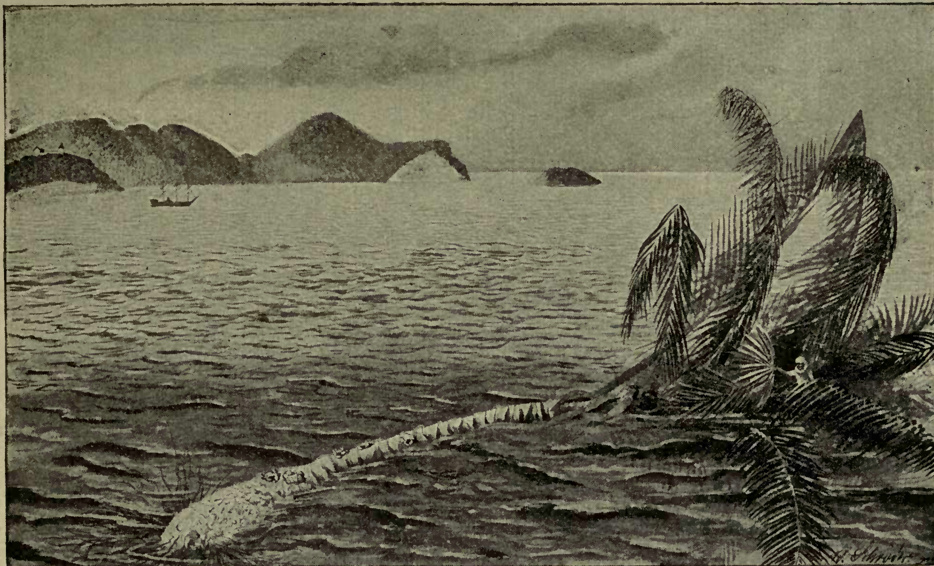

FIG. 4.—Palm-tree drifting in the open sea, a means of dispersal for fruit, seeds, or animals.
(*From Graebner's " Lehrbuch der Pflanzengeographie."*)

beach, some bearing living parasitic Fungi, and among these were numerous fruits of typical Malayan strand-plants. These, from the creeping *Ipomœa Pes-capræ* Sw., and *Vigna lutea* A. Gray, and the "tumble-grass," *Spinifex squarrosus* L., to Coco-nuts, *Pandanus*, *Barringtonia*, and lofty *Casuarina*, hung with vines, clothed the island from its shores far up its slopes, the forest-growth being in many places dense. The presence of five species of *Ficus* is attributed to fruit-eating pigeons, which, though they would probably eject any seeds within three hours of swallowing them, are capable of flying fifty miles in an hour.

CHAPTER V

PHYSIOGRAPHIC FACTORS

THOUGH it is certainly by their influence upon heat, light, rainfall, and drainage that the factors that we have here to consider chiefly influence plants, this influence is so obvious as to demand separate notice. The static, or more permanent physiographic, or topographical factors may be enumerated as altitude, slope, exposure, and surface. Dynamic forces in physiography, such as the weathering of rock-surfaces, their erosion by wind or rain, or the deposition of sediment over a surface, may also obviously cause important changes in the edaphic conditions of habitats.

ALTITUDE.—Altitude, measured generally from sea-level, affects temperature both of soil and air, and thus also the proportion of water that the air can hold without saturation, *i.e.* precipitation, and the amount of cloud. An important indirect effect is the period during which snow may cover the ground. That vegetation is distributed in zones or belts of altitude was the earliest scientific observation in the history of plant-geography. Mountains in equatorial regions bear successive altitudinal zones, belts, or girdles of climate and vegetation, which, at successive elevations, resemble the horizontal zones between the equator and the poles. Dense, hot, wet jungle, or "rain-forest," at their bases, gives way to more open forest, evergreen trees to deciduous, broad-

leaved trees, and these to conifers, dwarf Alpine shrubs, mosses, and lichens, and, finally, to perennial snow. As the snow-line falls gradually from 18,000 or 16,000 feet above sea-level in Equatorial regions to 14,000 and 11,000 feet in the Warm Temperate Zone; to 8000 and 4000 in Cold Temperate and Sub-Arctic regions; 2000 in the Arctic, and to sea-level in Polar regions, the actual altitudes of these zones will gradually diminish towards the Poles; while mountains in higher latitudes will, of course, start at their bases with the vegetation of the plain at that latitude.

The following nine altitudinal zones are recognisable on equatorial mountains:

1. *Zone of Palms and Bananas* (sea-level to 1900 feet), corresponding to the Equatorial horizontal Zone.

2. *Zone of Tree-ferns and Figs* (1900 to 3800 feet), corresponding to the Tropical Zone, with multitudes of Peppers, Aroids, and Orchids, the Figs replaced by arborescent *Urticaceæ* in the islands of the South Pacific, and Cinchonas being characteristic in the Andes.

3. *Zone of Myrtles and Laurels* (3800-5700 feet), corresponding to the Sub-tropical Zone, with Magnolias, Camellias, *Ericaceæ*, Evergreen Oaks, and other glossy, thick-leaved evergreens, and Acacias.

4. *Zone of Evergreen Trees* (5700-7600 feet), corresponding to the Warm Temperate Zone, with many showy *Leguminosæ*, *Myrtaceæ*, etc.

5. *Zone of Deciduous Trees* (7600-9500 feet), corresponding to the Cold Temperate Zone, but only represented, between the Tropics, on elevated plateaux.

6. *Zone of Conifers* (9500-11,500 feet), corresponding to the Sub-Arctic Zone.

7. *Zone of Alpine Shrubs or of Rhododendrons* (11,500-13,300 feet), corresponding to the Arctic Zone, with *Befaria* replacing *Rhododendron* in South America, and dwarf Willows, Junipers, and *Ribes* in the Himalayas.

8. *Zone of Alpine Herbs* (13,300 feet to the snow-line), corresponding to the Polar Zone, with vegetation in patches, chiefly of low-growing, wiry, large-flowered perennials.

9. *Zone of Mosses and Lichens* (above the snow-line).

Many factors interfere with the regularity of this zonation, such as the equalising influence of ocean surrounding such a mountain-peak as Teneriffe; the greater exposure

of one side of a mountain-chain to rain-bearing winds, as in the coast-mountains of Brazil, the Eastern Andes, the western slopes of the Western Ghats, and the south side of the Himalayas; and even the steepness of slope.

CLOUD.—The cloud-girdle, or zone, on a mountain where the air becomes super-saturated, which shifts its position upwards and downwards daily, has a marked effect. Its upper margin has night rainfall and sunshine by day; the lower margin both rainfall and shade by day. In the tropics it is the zone characterised by Bamboos.

DIRECTION OF MOUNTAIN-CHAINS.—The direction of mountain-chains is a factor of paramount significance, not merely because of its influence upon wind and rain, but also as affording possible pathways of migration. As the latitudinal zones of climate are already the greatest barriers to the northward or southward extension of the area inhabited by a species, mountain-chains running mainly east and west, such as the Himalayas and Central European ranges, may seem to bound floras, but will do little to assist in blending them. Ranges running mainly in meridional directions, however, such as those of America, East Africa, and Australia, extend a bridge across differing climatic zones which plants may traverse at varying altitudes with but little change in the climatic conditions to which they are accustomed. Thus it is suggested that the genus *Fagus*, originating in northern temperate latitudes, has made its way across the Equatorial Zone to form various species in the extreme south of America and Australasia.

SLOPE.—The angle of inclination or *slope* of the surface is, perhaps, mainly instrumental in determining the drainage and the rapidity with which humus, or other surface soil, is liable to be removed.

EXPOSURE.—Of greater import, perhaps, is aspect or exposure, whether a sloping surface faces to windward or to leeward, whether towards that point of the compass whence the sun shines, or towards that which is in shadow. The indirect effects of exposure, as, for example, through rainfall, can hardly be exaggerated. Mahabaleshwar, on the windward side of the Western Ghats, has 240 inches of rain annually, while Poona, on the leeward, has but 24 inches. The effect upon duration

of sunshine, or *insolation* as it is termed, and its results in evaporation and soil-temperature are also obvious.

SURFACE.—A factor of minor consequence is the

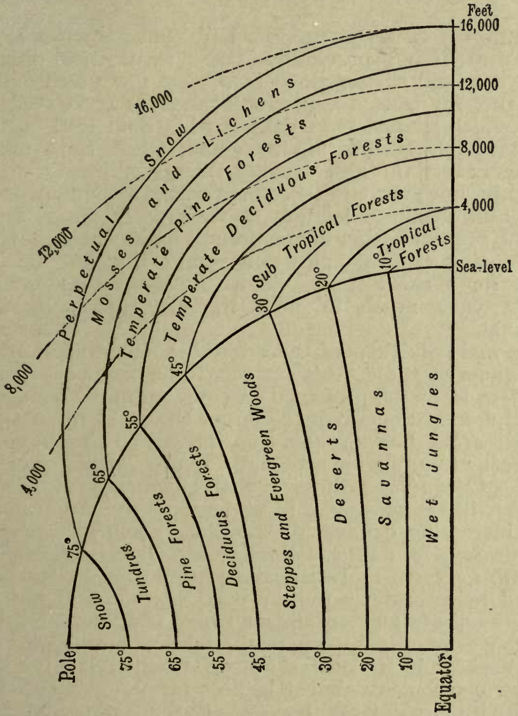

FIG. 5.—Vegetation-zones of latitude and altitude. (*By permission from Herbertson's "Outlines of Physiography."*—Edward Arnold.)

character of the surface, mainly as to whether it is even or uneven. Hummocks or slight irregularities may serve on a small scale as shelter for some low-growing species.

CHAPTER VI

BARRIERS

THE number of seeds produced by many species is so great that, if not prevented, any one of them might cover the land of the globe in a very few years. The Henbane, for instance, produces about 10,000 seeds a year, which, it has been calculated, would lead to the covering of the land within five years; whilst the average number of seeds of the Tobacco is thirty-six times greater. Not only, however, are there many risks attendant upon seeds and seedlings leading to their early destruction, but the preoccupation of the ground limits their chances of sprouting, and they may only retain their germinating power for a short time. As we have seen, moreover, species vary much in their mobility or facility of dispersal.

The main divisions of the Vegetable Kingdom occur in all regions of the earth's surface, though one Class, the *Cycadeæ*, is, at the present day, confined to the Southern Hemisphere. Several of the larger Natural Orders, such as *Compositæ*, *Leguminosæ*, *Cyperaceæ*, and *Graminaceæ*, also occur in all regions, though in very varying proportions. *Leguminosæ* diminish with increasing cold, *Compositæ* with increasing cold and moisture, and Grasses with increasing dryness of climate. Some few genera, such as *Senecio*, *Rubus*, *Plantago*, and *Oxalis*, are cosmopolitan, *i.e.* have representatives in all regions, the first named being noteworthy in that its thousand species present adaptations to almost every possible condition of climate or habitat, some semi-aquatic, many "weeds" of waste-lands ("ruderal") or woodlands, ivy-like climbers, succulent almost leafless forms, or shrubs, or trees with very large leaves. Though some aquatic species and herbaceous weeds of cultivated ground or of waste places are very widely distributed, few are even approximately cosmopolitan. The Shepherd's-purse (*Capsella Bursa-pastoris* Med. Pflan.) is nearly so. *Plantago maritima* L. occurs on our European shores, in Cape Colony, and at the southern extremity of America; and many Iceland species are found also in the Falkland Islands.

On the other hand, many species have an extremely restricted distribution, or small *area of distribution*. This is frequently the case with species in insular and mountain floras. This fact suggests that such species may have been evolved where they are now found. Their not having spread further may be attributed to immobility; and, when transplanted, they often do not refuse to grow elsewhere. The earth, in fact, by no means produces everywhere the species best adapted to each particular region, for introduced plants, such as Water-cress and *Trifolium repens* L. in New Zealand, will often oust native species.

Physical Barriers.—The distribution of most species and their power of *invading* new areas is, in fact, limited by *barriers*. These may be complete or partial, permanent or temporary, physical or biological. Among physical barriers we may class differences of climate and of soil, stretches of sea and, for aquatic plants, of land, wide rivers, deserts, mountain-chains, and masses of vegetation—in so far as their action is merely physical, as in retaining a large amount of stagnant water, or in producing a dense shade. Most of these physical barriers are of a permanent character.

Climate.—There is unquestionably no more potent factor in the separation of floras than differences of climate, by which, as we have seen, is mainly meant differences in the amount and seasonal distribution of atmospheric temperatures and moisture. As climates are limited horizontally and vertically, and species have but little power of acclimatisation, or adapting themselves to climates other than those to which they are habituated, each species may be said to have a poleward and an equator-ward or north and south limit—each being practically an isotherm—and a lower and an upper vertical limit. Migration will thus be possible to greater distances (unless other serious barriers intervene) in an east and west direction than meridionally. As there is no reason to suppose any great displacement of the Poles and the Equator—at least within those geological times with which we are concerned—it is easy to see that the vegetation of the earth must have always been separable into three great latitudinal zones or ancient floras—northern, tropical, and southern.

The *Northern* is now characterised by its needle-

leaved *Coniferæ*, growing in pure forest, its catkin-bearing, deciduous *Amentiferæ*, and a great variety of herbaceous types. The *Tropical* is characterised by dense, mixed forests, mostly evergreen, with arborescent *Polypetalæ*, especially *Leguminosæ*, *Meliaceæ*, and *Anonaceæ*, and gigantic Monocotyledons, including Palms, *Pandanaceæ*, *Scitamineæ*, and Bamboos, with numerous lianes and epiphytes. The *Southern* is now broken up into the widely distant floras of extra-tropical South America, South Africa, Australia, and New Zealand, which exhibit some original connection in the presence of *Restiaceæ* and *Proteaceæ*.

Soil.—Differences of soil explain many of the discontinuities of the occurrence of species within their areas of distribution, such as the absence of the calciphobe foxglove from Switzerland. In the important particular of water-content, habitats are very liable to undergo changes in course of time, as when an ironstone "pan" forms below a sand and obstructs its natural drainage, or when watercourses, partially dammed by a growth of *Sphagnum*, saturate or inundate the adjacent area. Soil-barriers are, therefore, not always permanent. A temporary drought may permit xerophytes to spread across ground naturally too wet for them, or a temporary inundation may entirely destroy certain species, so far as that locality is concerned.

Sea.—Even narrow straits may prove an insurmountable barrier in the migration of large-seeded plants, which would usually travel by successive short steps. Though many seeds will withstand the action of sea-water, some will not. Wind and birds may also act constantly in the wrong direction, or be inadequate to carry particular species.

Distance.—Here, however, distance, which must be considered as at least a temporary barrier, shows its effect. Whereas a chain of islands at no very great distance apart will act as temporary landing-places for migratory birds and for wind- or current-borne seeds, a wide stretch of uninterrupted ocean will act as a main obstacle to migration. For example, it has been estimated that from 75 to 90 per cent. of the species which "invade" new ground come from the immediately contiguous areas. Though, too (as we shall see more in detail in the next chapter), the floras of islands, even

the most remote from continents, consist largely of species indigenous to the nearest continent, the proportion of the species of the continent which succeeds in reaching the island is small, and consists mainly of forms with small, light seeds, or with fleshy fruits attractive to birds, or of strand-plants which can withstand the action of sea-water. Sea may, in fact, be said to form a barrier in proportion to its width. No species or even genus of Palms is, for example, common to the tropics of the Old and New Worlds. On the other hand, sea assists the distribution of marine Algæ, while the wider a mass of land intervening between two ocean areas, the less in common will there generally be between the Algæ of those seas. Even long and wide rivers, such as the Obi, serve to divide floras.

Mountain-chains.—Mountains that are lofty enough to transcend the vertical limits of any of those altitudinal zones to which reference has already been made will obstruct the migration of species belonging to lower zones, whilst snow-capped ranges will, of course, constitute yet more complete barriers. Macrotherms will have great difficulty in passing such a barrier. The direction of such mountain-barriers may be most significant. In Eurasia they run east and west, one result of which has been that the Tertiary flora, driven south by the increasing cold of the Glacial Epoch, had mainly to escape eastwards rather than southwards, and was largely exterminated, only one species of Palm, one Laurel, one Myrtle, and one Fig surviving in the Mediterranean flora of to-day. In America, on the other hand, the mountain-barrier running north and south, the warmer Tertiary flora represented by such genera as *Magnolia*, *Liriodendron*, *Liquidambar*, *Sequoia*, and *Taxodium*, was free to migrate southward, and to return as the climate once more improved.

Desert.—That a broad stretch of desert, with scarcely any water-supply save at rare oases, should act as an effective barrier to all plants except xerophytes is obvious. The Sahara forms a very complete barrier between the Soudanese and Mediterranean floras; but here a considerable difference of latitude is involved, and, for some distance also, the lofty range of the Atlas.

Vegetation.—A wide area of marsh, covered with its characteristic vegetation, although liable to be drained

by comparatively slight changes of circumstances, will offer an effective barrier against the spread of a xerophytic species; and in the same way the dense shade of a forest—apart altogether from its action as preoccupying the ground—will check invasion by sun-loving (*ombrophobe*) species. Such a forest-barrier would, however, be traversed if interrupted by open spaces.

BIOLOGICAL BARRIERS.—Among what are termed *biological barriers* may be reckoned the preoccupation of the ground, especially in the case of "close" or dense formations, such as the strong-growing social grasses of a meadow or the jungle or "rain-forest" of equatorial regions; the absence of suitable "host" species as limiting the occurrence of parasites; the absence of necessary pollinating insects, already alluded to; and the presence of serious fungal diseases. These will generally be but partial and temporary obstacles to migration.

As an example of the last-mentioned biological barrier mention may be made of the Larch-canker (*Dasyscypha calycina* Fckl.). This fungus occurs sporadically in the mountain home of the Larch; but in our moist plains the tree is less resistant, and the disease becomes epidemic.

CHAPTER VII

INSULAR FLORAS

No class of facts is of greater importance as illustrating the principles of botanical geography than that relating to the floras of islands.

Islands fall into two very distinct classes, differing widely in origin, geological structure, and the character of their native plants and animals. They are either *continental* or *oceanic*. The former are seldom at any great distance from the continent from which they have been severed. They are of varied geological structure, partly of stratified and partly of igneous rocks, and their plants are in the main identical with those of the continent. Continental islands are, however, subdivided into two subclasses, *recent* and *ancient*. Recent continental islands, such as the British Isles, Borneo, Java,

Japan, or the Philippines, are on submerged plateaux, seldom more than 100 fathoms below sea-level; while the ancient examples, such as Madagascar, the Greater Antilles, Iceland, Celebes, and New Zealand, are usually separated from the mainland by water of a thousand fathoms, or more, in depth, and may have a considerable proportion of "endemic" species or genera, *i.e.* of forms peculiar to them.

Oceanic islands, on the other hand, are generally remote from any continent; are either volcanic or coralline in structure and origin; surrounded by deep sea; and inhabited by a flora that is small in its total number of species, but has a large percentage of endemic types. The existence of these endemic types illustrates the importance of geographical isolation as a factor in the production of new forms. If only species, and not genera, are endemic, it seems probable that the origin of the island, or its covering with vegetation, does not date back very far. If they are of generic rank, such as the Double Coco-nut (*Lodoïcea*) of the Seychelles, it may be more ancient. At the same time such forms are not altogether isolated. *Lodoïcea* is related to the genus *Borassus*, Palms native to the continental regions of Africa and India. The most isolated type, perhaps, is *Lactoris fernandeziana* Phil., a genus and species endemic to Juan Fernandez, which has been made the sole type of a distinct Order. The rest of the flora of Juan Fernandez has, on the whole, a distinct Chilean facies; and the endemic forms of all oceanic islands show some continental affinities, while the non-endemic plants are, of course, common to some other land. This is not, however, always the nearest land, nor that from which ocean-currents or prevalent winds now come. In the Galapagos Archipelago almost every island has its own endemic species; the islands nearer to South America have forms more nearly allied to those on the mainland, while islands between others in position produce species intermediate in their characters. Affinity with a more distant land suggests that migration may have taken place at a more or less remote Tertiary period, when winds, currents, the outlines of continents, or the presence of intervening islands may have been different from what it is at present. Whilst the Galapagos flora is completely American, that of Kerguelen Land is more

akin to the flora of Fuegia than to that of the nearer African continent; and New Zealand, out of 935 species of Spermatophytes, has 677 endemic, 222 with Australian and 111 with American affinities. This last example illustrates the fact that the flora of an island is generally derived from more than one source. Even the British Isles, with a flora mainly "Germanic," or Central European, has Alpine species connected rather with Scandinavia, and at least one species (*Eriocaulon septangulare* With.) of American origin.

While continental islands will start with a flora composed of continental species, oceanic islands, beginning with no plants at all, will be gradually occupied by those which have the best means of dispersal. Low-lying coral islands will be mainly stocked by ocean-borne strand-plants; but volcanic islands, like Krakatau, will simultaneously receive, at higher levels, wind-borne and bird-borne species. The dependences of oceanic islands on occasional or accidental methods of introduction has a marked effect upon their floras. They are generally rich in species of Ferns, Mosses, and other Cryptogams, the excessively minute spores of which lend themselves to wind-dispersal. Whole tribes of plants, such as those with large and heavy seeds, are often absent. Not only is the total number of species smaller than on corresponding continental areas, but the proportion of species to genera is small, many genera being *monotypic*—represented, that is, by a single species. So, too, the proportion of genera to orders is small. This impoverished character of the flora lessens the intensity of the struggle for existence, so that ancient races—"living fossils," as they have been termed—may survive on islands when they have been exterminated elsewhere.

When the endemic species or genera "represent" those of the mainland, resembling them, that is, without being identical with them, it appears probable that they have originated in the island by modification of the continental type; and the degree of this modification—whether specific or generic—affords some evidence as to the antiquity of their origin.

In tropical and sub-tropical islands the effect of the insular climate is seen in the prevalence of woody, shrubby, and evergreen forms; whilst in those of higher latitudes herbaceous perennials predominate. Annual

plants being thus comparatively rare, and the whole flora, owing to the less intense struggle for existence, having been, perhaps, less forced to adapt itself to the environment, annual weeds, or other introduced plants, are often able to establish themselves with ease. They may spread at the expense of the indigenous or earlier flora. Thus the Dutch Clover (*Trifolium repens* L.) competes with the far larger New Zealand Flax (*Phormium tenax* Forst.): 269 introduced species in Mauritius, out of a total of 705, are largely exterminating the native plants; and in St. Helena introduced plants are doing even more than goats towards the extinction of the native flora.

The summits of mountains in islands of warm regions do not possess a true Alpine flora as do those of the continent. They are mostly characterised by a profusion of Ferns, and by the mere dwarfing of the species of the lower regions. This is explained by the absence of that ebb and flow of northern species under the advance and retreat of the Glacial Period which mostly affected the continents.

A comparative scarcity of flying insects to pollinate them, and the concomitant scarcity of conspicuously-coloured flowers, are said to be a feature of insular floras, whether continental or oceanic, the prevalence of high winds being supposed to explain the fact. In this, and in other characters, the distinction between continental and oceanic islands would seem, like that between insular and continental climates, to be one of degree rather than one of kind. Volcanic islands near the mainland may bear flowers differing no more from those of the mainland than do the floras of those detached areas of sedimentary rocks which we term continental. There is, in fact, a gradation in the proportion of an endemic element to the whole flora. So, too, what have been termed "harmonic" and "disharmonic" distributions graduate into one another, the former showing that development of large groups with many species characteristic, on the whole, of continents, while the latter shows gaps in series and many monotypic groups, the result of occasional introduction as opposed to wholesale migration.

The illustration of some of these principles will be found later on in the descriptions of some insular floras.

CHAPTER VIII

BRIDGES

THERE are difficulties in explaining plant-distribution, especially that of island floras, which are met in widely different ways by students of these questions. On the one hand, some writers, notably Darwin and Dr. Wallace, believing in the permanence of continents and oceans, at least in their main features, through most of geological time, and certainly throughout recent geological time, emphasise the possibilities of occasional means of transport to long distances. Unwilling to believe that land has existed where there is now deep sea, they point to the prolonged resistance that some seeds can offer to sea-water, the distance to which others may be carried by wind, the long flights of birds, and the possibilities of transport by floating tree-trunks or by ice-rafts. For them many islands have never been connected with the mainland.

On the other hand, many zoologists, and not a few geologists, argue in favour of very extensive changes of level resulting in land becoming water and water becoming land even in Tertiary times. This school believes that many volcanic and now remote islands have been connected with one or other of the continents, and that they have, on the whole, been stocked by ordinary migration, *i.e.* by short, not by long steps.

The questions at issue are largely geological and by no means simple. While it is urged that true oceanic islands are either coralline or volcanic and destitute of ordinary sedimentary rocks, it has been pointed out: (i.) that such rocks may be entirely masked by volcanic outpourings, and (ii.) that if such a continent as Africa were submerged, only a few peaks, mainly, if not entirely, volcanic, might be left exposed. While some writers do not hesitate to postulate great continental extensions, others content themselves with the suggestion of "bridges," which may have been narrow and isthmus-like, or even of chains of islands like the Antillean "festoon" which now extends between Yucatan and the mouth of the Orinoco.

ATLANTIS.—Some authorities still maintain the existence down to Miocene, if not to more recent, times of the great continental extension of land between North-west Africa and Ireland to which the name "Atlantis" has been applied. The Laurels of the Canaries, Madeira, and Azores, though belonging to a species now endemic, are one of the "Mediterranean" characteristics of their flora, and even more strongly recall the Tertiary fossil flora of Europe. The Euphorbias of the Canaries indicate the African affinity of their flora; but *Persea* and *Clethra*, while also Miocene, are now markedly American. It has, therefore, been suggested that these islands were connected by land both with America and with Europe, though a separation previous to the coming on of the Glacial cold allowed the Miocene genera and species to be retained with some variations of structural characters.

This suggestion appears unnecessary. The flora, though with its numerous Ferns and evergreens and considerable proportion of endemic species,[1] it is decidedly oceanic, is mainly of European affinities. The chief trees or shrubs, such as the Portugal Laurel (*Prunus lusitanica* L.), Myrtle, Laurestinus (*Viburnum Tinus* L.), *Myrica faya* Ait., Elder, Juniper, and *Laurus canariensis* Webb and Bert., all bear small berries, such as are eaten by birds, and all the birds of Madeira are European. If some genera surviving from Miocene times also survive in America, it is not that the Miocene flora was American, but that the American flora is Miocene. A similar close affinity exists between the floras of Eastern North America and Japan with their striking *Magnoliaceæ;* but it is not supposed that there has been a direct east and west migration between these two regions. More probably a flora existing in pre-Miocene times in the north has travelled southward along various meridians, and, becoming modified *en route*, now constitutes distinct but "representative" floras.

NORTH ATLANTIC BRIDGE.—This divergence of a Tertiary flora lends interest to the evidence for former land-connections between Labrador, Greenland, Iceland, the Faroes, Scotland, and Scandinavia, such as the

[1] In the Canaries 422 out of 977 species of Angiosperms, in Madeira 103 out of 648, and in the Azores 40 out of 478 are endemic.

extensive basalt-flows of early Tertiary (Eocene or Oligocene) date. This bridge seems to have been covered with forest, leaves of many trees, including *Sequoia*, *Taxodium*, *Platanus*, *Sassafras*, *Nyssa*, and *Magnolia* being preserved in associated beds of lignite and tuff.

Afro-South-American Bridge.—Whilst the great Permo-Carboniferous land-girdle known as Gondwana-land extended from Eastern Brazil southwards to the Falkland Islands, and apparently eastward to Guinea and northern Cape Colony, and so to the Deccan and Australia, it is supposed to have been interrupted in Jurassic times by subsidence in the Indian Ocean region, and also to have been narrowed by the encroachment of the South Atlantic in the Cretaceous period. A bridge, for which the name " Arch-Helenis " has been proposed, extending eastward from between the mouths of the Amazon and the La Plata, is believed to have lasted into Eocene times. Such a continuous tract of land or chain of large islands in Tertiary times, especially in conjunction with a similar connection between Natal and Madagascar and—by way of the Seychelles—with India, would elucidate much of the distribution of the tropical flora.

Antarctic and Australasian Connections.—Interesting problems of distribution are connected with the probable greater extension in previous times of the Antarctic Continent and the existence of land-connections between it and the other southern continental areas. The Antarctic land appears to be continuous, and is about twice the area of Europe, but is at present so completely ice-bound as to be all but destitute of vegetable life and of little apparent interest to the biologist. The ocean surrounding it is in general deep, but appears to present slight shallowings in the direction of the three main southern continental land-masses. While the plants of South Africa are only ordinally related to those of Australia, as by the *Proteaceæ*, the connection between America and Australasia is more intimate. The order *Proteaceæ*, which is, perhaps, a very early group of Angiosperms geologically speaking, is represented in Chile and Fuegia, is abundant in South Africa, is found in New Zealand and New Caledonia, and has numerous species in Australia restricted either to the eastern or western half of the continent. Such

genera as *Gladiolus* and *Crassula* also suggest a slight affinity between South America and South Africa; but it appears probable that there has been no direct connection between Patagonia and South Africa since Jurassic times. On the other hand, Patagonia and Argentina seem to have been joined to Antarctica during the Cretaceous period, by way of South Georgia, while the southern continent seems to have been simultaneously connected with Tasmania and Australia. A connection between Antarctica and New Zealand seems to have belonged to a different period; but, to allow of the migration of many plants from temperate South America to Australasia, these periods must have been characterised by far warmer conditions in Antarctic latitudes.

Whilst the flora of the Andes contains genera like *Ranunculus*, which may be considered as Scandinavian in origin, it has many remarkable distinctive types the range of which is noteworthy. *Fuchsia* and *Calceolaria* extend from Mexico to New Zealand. The Beeches, represented in northern temperate regions by a few species in Europe, Japan, and North America, and no longer found within the tropics, form a marked subgenus, *Nothofagus*, in Valdivia, Fuegia, Tasmania, Australia, and New Zealand; whilst the Oaks, so far more varied in the Himalayas and in the United States, only extend into the Southern Hemisphere in Java. *Gunnera*, *Acæna*, and the beautiful Winter's-bark (*Drimys*) are other Andine genera that extend into New Zealand, the last-named also reaching Tasmania. No less than one-eighth, and perhaps a higher proportion, of the New Zealand genera are, in fact, common to South America. Though more than one-third of the species are endemic and, with many "northern" genera, such as *Ranunculus*, *Epilobium*, and *Veronica*, New Zealand has many genera in common with Australia, the absence of such types as *Eucalyptus*, *Melaleuca*, *Grevillea*, *Hakea*, and the phyllodinous Acacias is remarkable.

The flora of Norfolk Island resembles that of New Zealand; but New Caledonia is far richer, having received a numerous immigration of tropical Indo-Malayan forms by way of Papua, the Solomon Islands, and the New Hebrides. So, too, Northern Australia has a Papuan element in its flora, represented by the wild Banana, Pepper, Orange, Mangosteen, Rhododendron,

epiphytic Orchids, and Palms; and these last are represented by *Rhopalostylis* even in New Zealand. Torres Strait is, even now, but a shallow and narrow separation. The evidence seems to favour a belt of more or less continuous "Melanesian" land from Papua to the Fiji Islands, and through the New Hebrides and New Caledonia to New Zealand; but the outer, or "Micronesian," chain, extending from the Philippines by the Pelew, Caroline, Marshall, Ellice, Samoan, and Cook groups to Tahiti and the Austral Islands, would seem to have been stocked by the ordinary transmarine agencies, currents, winds, and birds.

CHAPTER IX

MOUNTAIN FLORAS

ALTHOUGH on low hills the direct and indirect effects of altitude are not noticeable, in the ascent of mountains, especially in the tropics, the existence of successive altitudinal zones of climate and vegetation is very marked. The mistakes have been made of attempting to delimit these zones too precisely for the whole world, and of explaining them exclusively by the fall of temperature. The various changes that occur in the surroundings of plants in the course of ascent to successively greater altitudes may be briefly recapitulated:

1. Slope increases drainage and produces a marked contrast between periods of light ("insolation") and shade.

2. Up to heights at which the temperature does not become markedly cold, the amount of precipitation (rain) increases with altitude, and the air becomes consequently more humid.

3. Temperature falls at a rate which has been roughly averaged at 1° F. for every 300 feet until the snow-line is reached, above which the snow never completely disappears—a line the altitude of which rises from sea-level near the poles to about 2000 feet at North Cape, 4000 feet in Southern Norway, 8000 feet in the Alps, and 18,000 feet in the Himalayas.

4. Winds become stronger.

5. The air becomes more rarefied, and there is consequently greater radiation. Above the cold height previously alluded to (2) this results in a drying of the air, an absence of cloud, and a great reduction in precipitation.

6. Light is intensified.

7. The soil becomes progressively colder.

The responses of plant-form to these conditions are:

1. The general development of strong and deep root-systems and of the perennial habit.

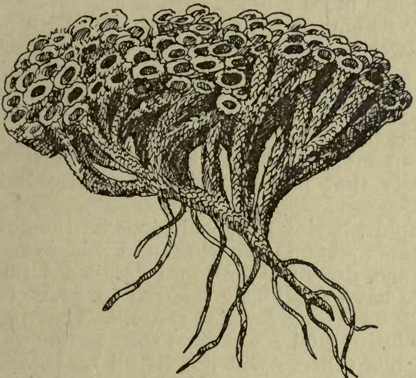

FIG. 6.—*Merope*, a Composite of the Higher Andes. (*From Graebner's "Lehrbuch der Pflanzengeographie."*)

2. The prevalence of woody plants, whether trees or shrubs, with a shortening of the internodes, more copious branching, and a stunted, more horizontal, or prostrate direction of growth (Fig. 6). Such wiry-stemmed "cushion-plants" as the Vegetable Sheep of New Zealand (*Rauolia*) and *Azorella* and many others in South America are very characteristic of wind-swept, sub-alpine plateaux.

3. Leaves are commonly smaller, evergreen, thick, and often inrolled at the edges, with few sunken stomata, and large air-spaces. These sclerophyllous characters may serve as protection against cold, and they certainly serve to minimise transpiration when, as a rule, the moist air and cold will lessen both it and food-absorption. At

the same time the large air-spaces will facilitate rapid transpiration when the temperature rises, and the evergreen condition will enable photosynthesis to occur whenever light and warmth are sufficient. The shortening of the leaf is characteristic of Alpine grasses. Tap-rooted herbaceous plants, such, for example, as the Dandelion and many Thistles, frequently assume the "rosette" habit, with leaves closely adpressed upon the soil.

4. Flowers are in many cases markedly larger and their colours more intense.

5. The whole surface may be shaggy with hairs, as in the Edelweiss.

With regard to temperature alone, mountains within the tropics clearly exhibit four zones, which may be described as *Tropical; Warm Temperate*, with a temperature averaging 60-70° F. and never falling below the freezing-point; *Cold Temperate*, where it sometimes falls below that point; and *Cold*, where it is usually below it.

Humboldt, basing his conclusions on the observations of Broussonnet on Teneriffe and his own ascent of Chimborazo, drew up the more detailed subdivision to which we have previously referred (p. 71.), giving mean annual temperatures for nine zones, and comparing them with the latitudinal zones from the equator to the poles. That such a scheme will not fit all cases, whilst some zones are clearly recognisable, almost vertically superposed, is well illustrated by the following passage from Sir Joseph Hooker's *Himalayan Journals:*

> "From the deep valleys choked with tropical luxuriance to the scanty yak pasturage on the heights above, seems but a step at the first *coup d'œil*, but resolves itself on a closer inspection into five belts. 1. Palm and Plantain. 2. Oak and Laurel. 3. Pine. 4. Rhododendron and Grass. 5. Rock and Snow. From the bed of the Ratang, in which grow Palms with Screw-pine and Plantain, it is only seven miles in a direct line to the perpetual ice."

The present writer has had a precisely parallel experience on the eastern slope of the Andes.

A more generally accurate subdivision, based upon moisture as well as temperature, and upon the vegetation as reflecting these conditions, is the following, taken, in the main, from Schimper:

Alpine Region	Upper, drier, desert to snow-line. Lower, grassland with drizzle.
	Upper limit of trees.
Montane Region	Moist, cold, resembling the lowlands of higher latitudes.
Basal Region	Moister, but not markedly colder than the plain, resembling moist lowland stations.

The two lower regions will be wooded, even more so than the plains below them. The cloud-belt extends over the Alpine grassland; but the wind is inimical to trees. Above the cloud-belt the dry cold air and soil produce the xerophytic conditions which, on lofty mountains, prevail immediately below the snow-line.

Obviously, mountains having their bases in higher, non-equatorial latitudes will not present the lower zones of vegetation of the tropics, but various local conditions will also modify their characteristics. An isolated volcanic peak, such as Teneriffe, surrounded by the equalising influence of the ocean, differs from continental mountains, such as the Alps; and the east and west extension of the Pyrenees or Himalayas gives them a very different relation to the vegetation at their feet from that of a meridional chain, such as the American Cordilleras. Thus, while the Himalayas divide the Central Asian xerophytic flora from the hygrophilous Indo-Malayan vegetation, there is said to be a recognisable "American" character in the flora of all latitudes of the New World, from Alaska to Fuegia. The genus *Befaria*, for instance, represents the Rhododendrons of the Old World from North America to Chile. At the same time, *Rhododendron*, represented by dwarf forms in Europe from Lapland to Gibraltar, but absent in Africa, is abundantly represented in the Himalayas and eastward in Yunnan, and takes advantage of a discontinuous meridional extension of mountainous habitats to appear under the form of *R. malayanum* Jack. in Sumatra, and even as *R. Lochæ* F. v. M. at 5000 feet on Mount Bellenden Ker, far down the line of the Australian chain.

Raised in isolation above the surrounding vegetation, mountains have been compared to islands. All mountains over 5000 feet in altitude, between 55° N. and 50° S., are, like islands, rich in endemic plants, both genera

and species. This is exemplified by the numerous endemic genera of the Andes, many of which are monotypic, or have but few species: in such isolated plants as the monotypic Passifloraceous *Guthriea capensis* Bolus, and the many endemic *Compositæ* and *Ericaceæ* on the Schneeberg in Cape Colony; and by the floras of Kilimanjaro and the Abyssinian Highlands. It is not a sufficient explanation of this large endemic element in mountain floras to say that it is due to the variety of station that mountains present. As in the case of islands, it would seem that isolation and its concomitant, a comparative absence of competition, have facilitated the origin of new specific forms.

The sub-Arctic mountains of Iceland, Scandinavia, and Kamtchatka do not yield the same wealth of endemic forms; but, in addition to these richly endemic mountain floras, we have, especially in the Northern Hemisphere, evidence—alluded to in one of our earlier chapters—of a flora originating in polar latitudes then warmer, driven south or east by the advance of Glacial cold, and, to some extent, returning as the climate improved. From this we have the curious result that some species of *Primula*, *Pedicularis*, and *Oxytropis* are now found only on the southern slopes of the Alps. (See Book I, chapter v.).

CHAPTER X

WATER-PLANTS

ALTHOUGH there are brackish-water estuaries in which marine Algæ mingle with shore Spermatophytes, the main practical distinction among water-plants is that between fresh and salt waters, which is approximately one between Spermatophyta and Algæ. Another distinction of primary significance is that between *Benthos*, or rooted plants, and *Plankton*, those that are free-swimming.

There are all degrees of transition between the herbaceous flowering plants that inhabit marshy ground and the water-side, and those which live in the water itself; so that aquatic Phanerogams may, in a wide sense, be termed an integral part of the land floras.

The total number of aquatic species of Spermatophytes is not large, and they mostly belong to a few, but very distinct, cohorts. Among Dicotyledons we have the *Nymphæaceæ* and Batrachian Ranunculi in *Ranales*, the *Podostemaceæ* among *Rosales*, the *Callitrichaceæ* classed with *Geraniales*, the Mangroves and *Trapa* among *Myrtifloræ*, *Villarsia* and *Menyanthes;* in the *Gentianaceæ* and *Utricularia* in *Tubifloræ*. Among Monocotyledons we have shore-plants, such as *Typha* and *Sparganium* in the *Pandanales*, the *Lemnaceæ* among *Spathifloræ;* and the one almost entirely aquatic cohort, the *Helobieæ*, including *Naiadaceæ*, *Potamogetonaceæ*, *Alismaceæ*, etc. These varied groups, having many terrestrial allies nearer than they are to one another, and yet possessing many parallel or representative characters that are obviously adaptations to their acquired habitat, it is clear that the aquatic habit has originated independently in these various cohorts. Though there are many Spermatophytes that vegetate under water, and not a few free-floating rootless forms, many too that ripen their fruits under water, flowering and pollination nearly always take place above or on the surface. The pollen and pollination generally suggest that these submerged plants are the modified descendants of land-plants. We cannot, in fact, point with confidence to a single Phanerogam as primitively aquatic. At the same time, the extreme modification of such entire orders as *Naiadaceæ*, *Ceratophyllaceæ*, and *Podostemaceæ*, which renders their systematic position doubtful, points, in such cases, to an extremely remote aquatic ancestry. Water has such high specific and latent heat that it is much slower than air to change its temperature. Aquatic plants are, therefore, little liable to have their growth checked by changes of temperature, or to be prevented from spreading over wide areas within the same zone of temperature. Almost all aquatics are consequently perennial, and they exhibit a general tendency to vegetative growth and multiplication, as opposed to sexual reproduction. Whilst in tropical waters this vegetative growth takes place uninterruptedly all the year round, in temperate latitudes the danger of destruction by the formation of ice at the surface leads to various forms of hibernation, such as the sinking of detached winter-buds.

The refraction of light by water gives to aquatic plants, even at moderate depths, the characters of shade-plants, such as long internodes, epidermal chlorophyll, and the absence of palisade-tissue. The buoyancy of the water renders such mechanical tissue as wood unnecessary, and the absence of transpiration and the absorption of food through the whole of the uncuticularised surface cause a great reduction in the vascular system. Even those water-plants that are rooted in the mud probably depend upon their roots for little beyond mere attachment. The general presence of large intercellular spaces, though it may serve to float the plant and thus aid it in obtaining air, is doubtless largely concerned in the storage of gaseous food-elements. The rounded leathery floating leaves, and the much-divided or long ribbon-like submerged ones, found often on the same plant, and offering a minimum of resistance to running water, are familiar external modifications occurring in many plants not otherwise related to one another.

The geographical distribution of aquatic Spermatophytes is far wider than that of average land-plants, especially in an east and west direction. Most British species range through the North Temperate Zone. In the remarkable tropical order *Podostemaceæ*, Dicotyledons resembling mosses or liverworts, adapted to life in rapid streams, and of most uncertain systematic position, *Podostemon* and *Tristicha* extend from Brazil to Madagascar and South Africa, the former also occurring in North America.

Although not so conspicuous by their size as are the Spermatophytes, the Cryptogamia contribute interesting types to fresh-water floras. Thus, in the *Benthos*, or submerged but rooted group, we have the *Characeæ*, so abundant on calcareous mud, such mosses as *Fontinalis* and *Hypnum* frequenting both running and stagnant waters, and the Quillworts (*Isoëtes*) of our lakes with their erect, rush-like leaves. In the *Pleuston*, or free-swimming group, such Hepaticæ as *Riccia*, and *Hydropterideæ* such as *Azolla* and *Salvinia* occur with Duckweeds (*Lemna*), *Utricularia*, *Aldrovanda*, etc. The green Algæ or *Chlorophyceæ*, which are of very primitive construction and cosmopolitan in occurrence, include many rooted forms and others that are free-swimming. The *Plankton*, or floating micro-organisms of our lakes,

estuaries, and seas, consists, so far as plants are concerned, mainly of microscopic representatives of this group and of the Diatoms. It is noteworthy that these world-wide groups of simple organisms occur in fresh, brackish, and salt waters, that they are entirely submerged, and that their chief reproductive structures are free-swimming ciliated zoospores and spermatozoids. These characters point to the Algæ being primitively aquatic; and the production of ciliated spermatozoids by the gametophyte of the now mainly terrestrial Bryophyta and Pteridophyta suggest a similarly aquatic ancestry for those phyla of the vegetable kingdom.

When we turn to marine aquatics we find them almost entirely Algæ. There are but twenty-seven known species of marine Phanerogams, of which the best known are our Eel-grasses or Grass-wracks (*Zostera*). No flowering plants are so completely adapted to an aquatic life as are these ancient types of Monocotyledons. They produce a dense network of rhizomes in the mud of gently sloping shores, and bear long, narrow, ribbon-like leaves and a flattened spadix, the anthers on which burst under water, discharging long tubular pollen, which is carried by the water to the thread-like and equally submerged stigmas.

The Algæ, exclusive of the Diatoms, which, as we have seen, contribute to the *Plankton* of both salt and fresh waters, fall into three main groups. Of these the green *Chlorophyceæ* are mainly fresh-water, while the red *Florideæ* and the larger, leathery, olive-brown *Melanophyceæ* are almost exclusively marine.

The marine flora shows no such geographical diversity as does that of the land. Drude has, however, divided it into three main "Domains," corresponding to the primary divisions of the land, Northern, Tropical, and Southern. The Northern, extending down to about 41° N. lat., is the region of *Laminaria*, *Alaria*, and *Fucus*. *Laminariæ* in Arctic seas reach a length of 65-80 feet, *Alaria* furnishes some of our edible species, while *Fucus*, the Bladder-wracks, are familiar on all our coasts. The Tropical Domain, with which is included the Mediterranean, is the region of *Sargassum* and the *Florideæ*, and the Southern Domain that of the gigantic Kelps, *Macrocystis* and *Durvillæa*.

Bathymetrical Distribution.—Depth is to the

distribution of Algæ what altitude is to that of mountain floras, light playing a part similar to that played by heat in the other case. An Upper Littoral Zone extends down to low-water mark; a Lower Littoral Zone may be traced down to a depth of 60-90 feet (10-15 fathoms). Beyond this light is almost absent, and with it disappear all the larger Algæ.

BOOK III

FLORISTIC REGIONS

CHAPTER I

THE NORTHERN ZONE

The surface of the globe is, as we have seen, divided into three main zones, so far as the incidence of light and heat are concerned, Northern, Tropical, and Southern. The differing capacities for light- and heat-absorption of land and water, and the interference of land-masses modifying the courses of ocean-currents, prevent these zones from coinciding with lines of latitude. In area of land they are very unequal, the Northern comprising most of the great belt of almost continuous land surrounding the Arctic Ocean, whilst the Southern includes only the narrowing southern portions of South America and Africa, half of Australia, New Zealand, and the now barren Antarctica.

The most striking features in the Northern Zone as a whole are its pure forests of needle-leaved Conifers, catkin-bearing and other deciduous Dicotyledons, and numerous herbaceous species. Still mainly considering temperature, we may divide it primarily into three sub-zones, the Arctic, Northern Temperate, and Southern Temperate. Of these, the *Arctic Sub-zone* constitutes one fairly homogeneous floristic region extending down to lat. 52° N. in Labrador, but ending rather north of the Arctic Circle in Europe, its southern boundary being the northern limit of trees.

Arctic Region.—The *Arctic Region* is characterised by its long cold winters, when the sky is clear, there is but little precipitation, and strong dry winds sweep away the scanty snow; and by its short summers, when, owing to the low altitude of the sun, the temperature is cool, but fogs are frequent. The whole period of vegetation

is thus crowded into six or eight weeks, annual plants are all but absent, and many of the prevalent herbaceous perennials do not ripen seed. Large low-lying areas are covered by mosses and lichens, the latter predominating on the poor porous sand derived from granitic rocks and constituting *dry tundra*, whilst the mosses may or may not retain more moisture and form *wet tundra*. Three factors, the continuous daylight during the period of vegetation, the low temperature, and, above all, the cold of the soil, combine to retard growth, and the 800 species of this region are consequently mostly low-growing

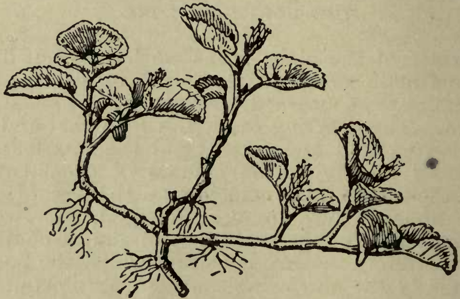

FIG. 7.—*Salix polaris*, the Dwarf Arctic Willow (nat. size). (*From Graebner's "Pflanzengeographie."*)

and xerophytic. Many of them, such as the Saxifrages and *Papaver nudicaule* L., assume a cushion-like habit; have leathery, cuticularised leaves, as in the cases of *Andromeda tetragona* L., or *Diapensia lapponica* L.; or become succulent like *Saxifraga oppositifolia* L.; hairy, as are *Dryas octopetala* L., *Loiseleuria procumbens* Desf., and *Salix lanata* L.; or coated with wax, as is *Salix reticulata* L.; or have their leaves rolled up, as in *Hierochloe alpina* Rœm. and Schul. Numerous and relatively large flowers are the rule; but few are scented. Characteristic types, in addition to those already mentioned, are *Cladonia rangiferina*, the Reindeer-moss lichen, species of *Polytrichum*, *Empetrum nigrum* L., *Carex*, *Ranunculus*, *Pyrola*, *Eriophorum*, and *Poa*. The most numerously represented orders are *Cyperaceæ*, *Gramineæ*, *Caryophyllaceæ*, *Cruciferæ*, and *Compositæ*.

Five-sevenths of the species of the Arctic region occurring in the mountains of Scandinavia, the flora has been termed "Scandinavian"; and, driven southward by the cold of the Glacial Period, it has so far invaded the mountain-heights of continental areas, even crossing the Tropics, that it has been said to be represented in all latitudes, and is often named "Arctic-alpine." Hardly any of the "alpine" plants of the Tropics belong, however, to Northern species.

Northern Zone of Cold Winters.—The *North Temperate Sub-zone*, also known as the "Northern Zone of Cold Winters," or region of "Summer Forest," extends from the northern limit of trees to about lat. 50° N. (the southern border of Siberia) in Asia, to the centre of European Russia, the Eastern Carpathians, Balkans, Alps, and Pyrenees in Europe, whilst in North America it comprises Southern Alaska, British Columbia, most of Canada, and the North-eastern, Central, and North-western United States. Here, though the climate varies from "insular" on the west coasts to "continental" towards the east, there is no real dry season, and the soil is in general permanently moist from the evenly-distributed rainfall. The period of growth lasts from three to seven months, with its maximum in July; the summers are not so dry as to parch the vegetation, but the winters are so cold as to check growth, and the broad-leaved Angiospermous trees are mostly tropophilous, *i.e.* they shed their leaves, develop cork, and diminish transpiration in that half of the year, so that they form "summer green" forests.

The sub-zone has been divided into the *Europæo-Siberian* and *North American Forest Regions*, its distinctive feature being the vast areas originally occupied by forests, either "pure" or homogeneous, or made up of few species of trees. On the whole, the colder northern or higher districts are occupied by Conifers, especially *Pinus*, with evergreen xerophytic leaves and little undergrowth; the milder southern or lower districts by deciduous catkin-bearing Dicotyledons, such as Oaks, Beeches, Chestnuts, and Maples. The most northern Conifers, the Larches, are, however, deciduous; the broad-leaved Birches extend beyond the Conifers both in latitude and altitude; and on sandy and peaty soils Conifers are characteristic even in the south. The

undergrowth of the deciduous forests comprises shrubs, such as Hazel, Blackthorn, Hawthorn, and Holly; some woody climbers, such as Ivy and Honeysuckle; but no true lianes or epiphytic flowering-plants; Ferns, never arborescent, occasionally growing on the trees, as do many Lichens, Mosses, and Algæ; Grasses and many spring-flowering herbaceous perennials, such as our Primroses, Wild Hyacinths, Wood Anemones, etc.

Immense areas in some parts of this sub-zone are covered by heaths, where a few species, such as *Calluna vulgaris* Salis., *Erica*, and *Vaccinium*, predominate. Natural turf or meadow, composed mainly of perennial shallow-rooted Grasses, which die down in winter, but comprising also Sedges in wetter ground, and members of many other Orders, and alder-fens are also striking features of the Europæo-Siberian Region. In the park-like regions of Kamtchatka, *Heracleum*, *Angelica*, and other herbaceous *Umbelliferæ* reach a gigantic size.

The flora of the United States has been analysed into three components, endemic, European, and Asiatic, its distribution being mainly meridional. While the European components are most numerous in the east, those from Asia are also more numerous on that side than on that nearer to Asia, several Japanese genera, especially the *Magnoliaceæ*, being represented in the Eastern States. The mountains of north-east Asia seem to have escaped glaciation and to have served as a centre of radiation both in this direction and into Europe.

CHINO-JAPANESE REGION.—Much of Japan and north-eastern China, having an equable rainfall, should probably be classed in this sub-zone; but its forests have been destroyed and the character of much of the country altered by irrigation, so that wild plants exist only in the mountains. Among the most interesting endemic forms are the coniferous *Cryptomeria* and that remarkable ancient and now isolated Gymnosperm *Ginkgo biloba* L.

The main Chino-Japanese Region, however, with a monsoon climate giving a rainy spring, is remarkable for its well-marked flora, distinct from that of the Steppe Region, continuing westward into the Eastern Himalayas, and presenting the interesting affinity with that of the Eastern United States already mentioned. It contains no *Cistus*, only one species of *Ferula*, the comparatively

small number of 35 species of *Astragalus*, 2 of *Pistacia*, and 4 of *Clethra*. On the other hand, of the genera most represented in Sikkim it has 134 species of *Rhododendron*, 129 of *Pedicularis*, 77 of *Primula*, 76 of *Corydalis*, 66 of *Quercus*, and 58 of *Saxifraga*. Its most characteristic Order, the *Camelliaceæ*, are represented by 71 species, *Acer* by 42, *Vitis* by 35, and the *Magnoliaceæ* by 33, including a *Liriodendron*. In its wealth of species and in not a few characters it suggests comparison with the Mediterranean Region.

NORTHERN ZONE OF HOT SUMMERS.—The *South Temperate Sub-zone*, known, so as to be distinguished from a division of the Southern Zone, as the "Northern Zone of Hot Summers," may be taken to include the islands of the North Atlantic, the Azores, Canaries, and Madeira, the Mediterranean, North African, Levantine, Steppe, and Central Asian Regions in the Old World, and the Prairie and Californian Regions in North America. Its climate is more extreme than that of the sub-zone to the north of it; and, though there is no real winter, grass is parched in summer. Most of the vegetation is xerophytic. Needle-leaved *Coniferæ;* evergreen trees and shrubs, often "sclerophyllous," *i.e.* with rigid leathery leaves; and, in the driest regions, succulent plants, are characteristic.

The Azores, Madeira, and the Canaries, all volcanic and rich in endemic species, form three distinct archipelagos, although their flora is known collectively as "Atlantic." The Bruyère or Tree-heath (*Erica arborea* L.), species of *Laurus*, and a wealth of Ferns, are characteristic of all of them. With 40 endemic species, out of a total of 478, the Azores are in the main European and Mediterranean. Madeira, with 103 endemic species out of 648, but with its wild plants largely exterminated by cultivation, preserves Tertiary types in *Clethra arborea* Ait. and the sapotaceous *Sideroxylon*, and African connections in *Dracæna Draco* L. The Canaries, with a larger endemic element (422 species out of 977), are far more African. Their lower ground, where species of Date-palm, Tamarisk, and *Euphorbia* all bear the specific name *canariensis*, especially exhibit this relationship. Above this, *i.e.* from 1600 or 2600 feet up to 4000 feet, is the belt of evergreen *Lauraceæ*, *Laurus canariensis* Webb and Bert., *Persea indica* Spreng., and *Ocotea fœtens*

Benth. and Hook. with *Myrica Faya* Ait. From this to nearly 6000 feet is the belt of Conifers and Heaths; and above this again the Retama (*Spartocytisus nubigenus* Webb and Bert.). It is noteworthy that on the lofty volcanic heights of these islands, where botanists first traced altitudinal zones in detail, there is none of the so-called "Scandinavian" invasion of Glacial times.

The *Mediterranean and Levantine Region* is remarkable for the dense scattered thickets or *maquis* (Italian *macchia*) of fragrant glandular and often prickly shrubs with rigid leaves, such as *Myrtus communis* L., *Pistacia Lentiscus* L., and *Laurus nobilis* L.; for the Olive (*Olea europæa* L.), Evergreen Oaks (*Quercus Ilex* L., *Q. Suber* L., etc.); for numerous sweet-scented *Labiatæ;* and for the Fan-palm (*Chamærops humilis* L.), which is wild on both sides of the Mediterranean. The Date-palm, though grown in Italy, belongs to the oases of the Saharan region. The desert districts of Syria and Palestine, with their few Tamarisks and spinous Acacias, form a transition to the next region.

The *Steppe and Central Asian Region* stretches from the Danube to the upper Amoor and from the Volga to the Persian Gulf and the Himalayas. Throughout this immense area there prevails a regular succession of three marked seasons, a long and severe winter with snow, a short spring, and a rainless summer. The vegetation is consequently typically xerophytic with bulbs, spines, or dense coverings of hair. Salt plains are frequent with characteristic "halophytic" vegetation, especially *Chenopodiaceæ,* such as the bushy Saxaul (*Haloxylon ammodendron* Bunge). Shrubby species of *Astragalus* and the genera *Rheum* and *Ferula* are also well represented (Fig. 8). These wind-swept plains and plateaux are unsuited to any tree-growth.

The *Prairie Region* of North America, in many respects a similar area, is a treeless plain with an extreme climate, short spring rain, and dry summer. The prevalent west wind from the Pacific condenses all its moisture on the Rockies, and the rivers that do originate from its rainfall flow in deep cañons, so as to be of little use for irrigation. In its northern portion this region is a true grass steppe, parched in summer: in the south-west, the salt or "alkali" desert, with its Sage-brush (*Artemisia tridentata* Nutt.) and the Creosote-scrub (*Larrea mexicana*

Moric.) passes into the "Mezquit" of spinous Acacias (*Prosopis*), forming, with other thorny shrubs, what is known as "Chapparal," much the same as the "maquis" of the Mediterranean. Indicative apparently of the former extension of a warmer climate northward, *Agave*, *Yucca*, and Cacti abound from Arizona and Texas into Mexico, the "Highland" region of the latter

FIG. 8.—*Rheum nobile* Hook. fil., from steppes of Sikkim, in Edinburgh Botanical Garden.

country, above 5000 feet, being, in fact, a mere southward extension of this region.

The *Californian Region*, west of the Rocky Mountains, with but little difference in temperature between summer and winter, and with no rain in the former season, much resembles the Mediterranean. From the north, and in higher ground, are the gigantic conifers, the Sequoias, the loftiest species in the world, the Douglas Spruce (*Pseudotsuga Douglasii* Carr.), and various Pines, recalling the Cedars of Lebanon and Atlas and the Corsican and Aleppo Pines; whilst evergreen broad-leaved trees,

and the cultivation of Maize, Wheat, Oranges, the Vine, the Olive, and many other fruits, serve to maintain the parallelism of the two regions.

In striking contrast to the rest of the zone in which they occur are the small areas in the Northern Hemisphere of what are known as the *Temperate and Sub-tropical Rain-forests*. The former was represented in Southern Japan; but, except in the temple-groves, has been destroyed by cultivation. It consisted largely of lofty evergreen Oaks of various species growing socially, but with Camphor and other evergreen *Lauraceæ*, *Camelliaceæ*, etc., woody lianes, a few epiphytic Orchids and Ferns, and parasitic *Loranthaceæ*; and it formed the northern limit of many tropical Indo-Malayan families, such as *Meliaceæ*, *Melastomaceæ*, *Begoniaceæ*, and *Piperaceæ*.

The sub-tropical rain-forest is but an extension of the tropical rain-forest beyond the tropical zone, as in the lowlands of Northern Mexico, Louisiana, and Southern Florida. Here again evergreen Oaks (*Quercus virginiana* Mill.) predominate, hung with the grey festoons of the epiphytic *Tillandsia usneoides* L., and other species, with climbing Aroids and Figs, Magnolias, Sabal-palms, mostly dwarf, and but few woody lianes. In swampy ground the Oak gives place to the Bald or Deciduous Cypress (*Taxodium distichum* Rich.), and on sandy tracts to the Pitch Pine (*Pinus palustris* L.) and other species.

CHAPTER II

THE TROPICAL ZONE

An example of the modification of heat-distribution by that of moisture as striking as that above-mentioned is afforded by the contrast between the tropical desert regions of the globe and the rain-forest areas of latitudes not greatly different. Several of the great desert regions extend, it is true, considerably beyond the lines of the Tropics poleward; but they are certainly in latitudes where the total annual supply of heat is sufficient for all purposes of plant-life. The character of their vegetation is determined by the minimum of water-supply.

Saharan Region.—The greatest desert in the world, the *Saharan Region,* represented, as we have seen, in the Canary Islands, extends across Africa, between the parallels of 20° and 35° N., Arabia, Southern Persia, and Baluchistan to Sind. It is exposed to the unchecked prevalence of the north-east trade-wind, and its incoherent soil, stony or sandy, is often blown into dunes. Sparse and stunted as is its vegetation, plants are not absent. Where scanty spring rain occurs, shallow-rooted annual species of *Malcomia, Rœmeria,* and *Astragalus* spring up, with the Rose of Jericho (*Anastatica hierochuntica* L.) and the water-storing Ice-plant (*Mesembryanthemum crystallinum* L.), a member of the characteristically desert family the *Aizoaceæ.* Some of these, though apparently hygrophilous, are only enabled to survive by the enormous distance to which their roots spread horizontally. Such, for instance, is the case with the annual gourd *Citrullus Colocynthis* Schrad. Other plants are more obviously xerophytic, being mostly very deep-rooted shrubs dependent upon those subterranean waters which rise to the surface in the springs of the oases, the home of the Date-palm (*Phœnix dactylifera* L.). Among these are spinous Acacias, such as *A. Seyal* Del.; *Alhagi,* the Camel-thorn; *Zygophyllaceæ,* such as *Nitraria, Zizyphus Spina-Christi* Willd.; the broom-like *Genista Rœtam* Forsk.; *Capparis spinosa,* coated with wax; *Atriplex Halimus* L., covered with vesicular hairs; cactus-like Euphorbias; erect shrubby and prostrate species of *Convolvulus;* Grasses with inrolled leaves, such as *Cynodon Dactylon* Pers.; bulbous species of *Ornithogalum, Allium, Urginea,* etc.; the fleshy Stapelias, with their evil-smelling fly-haunted blossoms; and many species with fragrant ethereal oils, balsams, gum-resins, and exudations of gum. Such are the species of *Ferula,* the gum Acacias, and the incense-yielding *Boswellia* and *Balsamodendron,* which gave to the southward extension of this region into Somaliland and Southern Arabia the name of the "Region of Balsamic Trees."

Central Asian Desert.—This desert is almost continuous, through that of Syria and Mesopotamia, with the great Central Asian desert, which is entirely extra-tropical and has an extreme climate. It consists of the plains between the Caspian and the Thian-Shan Moun-

tains, and the desert-plateaux of Tibet, the Tarim, Dzungaria, and Gobi. The Chenopodiaceous *Haloxylon;* many species of *Astragalus;* the grey-green *Artemisia,* torn up into "wind-witches" by the unchecked gales characteristic of deserts; shrubs such as *Tamarix* and *Reaumuria;* spinous plants such as *Alhagi camelorum* Fisch., *Xanthium spinosum* L., and *Eryngium campestre* L.; bulbous species of *Allium,* and in Dzungaria of *Tulipa;* species of *Rheum;* and, in Tibet, dwarf *Hippophaë* and *Potentilla,* make up the scanty flora. In the oases is an interesting assemblage of familiar types, Poplars, Ash, Elm, Willow, Raspberry, etc.

North American Desert.—In North America also desert conditions extend far north of the line of the Tropic, both where the rainfall is intercepted by the various Cordilleran ranges and so shut out from the "Central Basin" of Nevada, Utah, Western Arizona, and Southern California, and where an extremely permeable soil drains off what rainfall there is, as in the "Bad Lands" of South Dakota and Nebraska. On the far loftier Mexican Highlands to the south, though there is some snow in winter, there is but little summer rain, and the added desiccating effect of altitude produces conditions and vegetation similar to those of the north. As in the Sahara, there is, from February to April, a short-lived rain-flora; but the more permanent vegetation is typically xerophilous. Reduced leaf-blades, hairiness, and spines are as prominent as in Old World deserts, of which we are also reminded by species of *Atriplex, Lycium,* and *Artemisia. Sarcobatus vermiculatus* Torr., *Suæda,* and other *Chenopodiaceæ; Plantago; Aster* and many other *Compositæ;* spinous *Prosopis;* the "Pepper-grass" (*Lepidium intermedium* A. Gray); *Eschscholtzia; Cucurbita,* and interesting northward extensions of the South American *Loasaceæ* are characteristic. It is, however, by its Cacti, Agaves, and Yuccas that this region is rightly best known. *Opuntia* and *Cereus* extend northward; *Echinocactus* is more southern; *Yucca* belongs emphatically to the high ground; whilst *Agave* and *Fourcroya,* the arborescent liliaceous *Dasylirion* and *Beaucarnea,* with various species of *Sedum* and *Echeveria,* are mainly Mexican. The remarkably close identity of outward form and vegetative structure between the Cacti, with fluted fleshy stems

and spines for foliage, and the *chevaux-de-frise* of pointed fleshy leaves of the Agaves of this region on the one hand, and the Euphorbias and Aloes of Africa on the other, is the classical example of "representation," when that somewhat overweighted term is used in the sense of mere parallelism of adaptation. This is, of course, quite a different thing from the representation of one species in one area by an allied one in another, which may mean descent from a common ancestor and modification following isolation.

Between the three great meridional or continental divisions of the humid Tropical Zone, the African, Indo-Malayan, and American, there is little, if any, of that affinity, suggestive of recent migrations, that we have seen among the divisions of the Northern Zone. For example, though Palms and Orchids occur in all three divisions, there is no genus of Palms and there are very few genera of Orchids common to the Old and New Worlds.

In no part of the zone is vegetation liable to be checked by cold; but with regard to precipitation there are two main conditions: (i.) the almost perennial rainfall of the equatorial rain-forest, with heavier falls at the two seasons when the sun is vertically overhead; and (ii.) the existence of a dry season of three months or more, producing the "savannah" and "caatinga" formations, with distinctly xerophytic vegetation. This latter condition occurs markedly in Eastern Equatorial Africa, Western Australia, Venezuela, and Southern Brazil. It is characterised by tall grasses; scattered trees, some of which are deciduous, while others may have swollen barrel-like stems; numerous large Euphorbias or Cacti; some Acacias, and few lianes or epiphytes.

Tropical Rain-forest.—In the *Tropical Rain-forest*, as we have it in Western Equatorial Africa, Southern Ceylon, Southern India, the Malay Peninsula and Archipelago, North Australia, and the Amazon valley, the Vegetable Kingdom is seen in its greatest richness of variety and luxuriance of growth and energy. A large proportion of the species are arborescent, and the trees forming the forests are of many species, rarely social, so that no one is dominant, and have mostly straight stems, reaching a height of 50-100 feet or more, with their branches and evergreen foliage spreading in a close

canopy overhead. Unbranched Tree-ferns and Monocotyledons, such as Palms, Bamboos, and Plantains, are abundant; the stems of others often have prominent vertical buttress-roots, as in the Silk-cotton trees (*Eriodendron*); and the whole jungle is interlaced with a tangle of woody climbers or lianes, such as *Ficus, Bauhinia, Bignonia, Paullinia,* and *Lygodium.* Epiphytic Aroids and Orchids cover the boughs, and parasites are also numerous. The leaves are often leathery and glossy: they often taper into "drip-tips," and in the shade are often red, especially on their under surfaces. Flowers and fruit are often borne on the main stem, from dormant buds. The ground is often carpeted with ferns, especially *Hymenophyllum,* or *Selaginella;* but there is a general absence of greensward.

The following Orders are mainly restricted to this zone, which is estimated to comprise two-fifths of the land of the globe and to have also two-fifths of the Phanerogamia: Anonaceæ, Menispermaceæ, Bixaceæ, Guttiferæ, Bombaceæ, Malpighiaceæ, Simarubeæ, Burseraceæ, Meliaceæ, Cæsalpineæ, Passifloraceæ, Ebenaceæ, Gesneraceæ, Artocarpeæ, Pandanaceæ, Zingiberaceæ, and Marantaceæ. Dipterocarpaceæ and Nepenthaceæ are confined to the Indian Monsoon Region, Pandanaceæ to the Old World, and Cinchoneæ, Lecythideæ, Marcgraviaceæ, and Cyclanthaceæ to South America.

Mangrove-swamps.—A striking characteristic of the humid portions of the Tropical Zone is the occurrence of Mangrove-swamps along its coasts. A few species of trees, belonging chiefly to *Rhizophora, Avicennia,* and *Sonneratia,* grow on saline tidal mud-flats, supported on spreading "flying-buttress" roots from their main stems, and "pillar" roots descending vertically from their branches. They have also ascending aerating roots, like the "knees" of the Deciduous Cypress of Louisiana. Their seeds are often "precocious" or "viviparous," germinating while still in the undetached fruit and at once forming a long radicle by which, on falling, they are anchored in the mud. Growing in salt water, Mangroves are distinctly xerophytic, their leaves being leathery, with a thick cuticle. On sandy shores, both in the Old and New World tropics, the Mangrove-swamp is commonly replaced by the wide-spreading runners of *Ipomœa Pes-capræ* Roth. Further inland, where the

tidal water is less saline, we have in the east the Nipa-formation, consisting mainly of the "stemless Palm," *Nipa fruticans* Thunb., and, about tide-level, very often a forest in which *Barringtonia speciosa* L. fil., which has a floating fruit, is the dominant species.

The tropical forests themselves are divisible, according to the amount of moisture, into four grades: High Rain Forest, High Monsoon Forest, Low Savannah Forest, and Low Thorn Forest.

High Rain Forest requires over 72 inches of rain annually. Its trees exceed 100 feet in height, are evergreen, and distinctly hygrophilous in type. Though they do shed their leaves periodically, this periodicity is quite independent of climate or season, and sometimes differs on different branches of one tree. On the other hand, all the plants in a district will, in the case of some species, flower on the same day. Buttress-roots are common, and thick-stemmed lianes, among which are Palms, and the groups mentioned above; and the epiphytes include not only Ferns, Lycopods, and herbaceous plants, but also woody species.

The *Monsoon Forest* has from 60 to 72 inches of rain, or more, but with a definite dry season. Its trees are less lofty, tropophilous in character, many of them distinctly deciduous, and the epiphytes do not include woody plants.

The *Low Savannah Forest* has generally a rainfall of between 36 and 60 inches a year; but its occurrence depends partly upon edaphic conditions, its soil being necessarily retentive. Its trees are not more than 65 feet in height, are rarely evergreen, and distinctly xerophytic in character. Among them may be some with barrel-like water-storing stems, for which the African name "Baobab" may, perhaps, be generalised. Growing in open order, the forest is poor in underwood; but its soil permits the lofty grasses that are so distinctive of savannah conditions; and the trees may bear both herbaceous lianes and epiphytes.

The *Thorn Forest*, for which some authors would employ the Brazilian name "Caatinga," with even less rainfall and a non-retentive soil, is even more markedly xerophytic in the generally thorny character of both its trees and their undergrowth, and in the general absence of all epiphytes.

Africa.—The ancient, long consolidated, undisturbed, and isolated continent of Africa is as remarkable for the elements that are absent from its flora as for what it possesses. As the "Scandinavian" forms have not got across the Mediterranean to the Atlas Mountains, so neither do the European Miocene types seem to have reached it. It has neither *Magnoliaceæ* nor Maples, no *Rhododendron, Vacciniaceæ, Pomaceæ*, or *Quercus*. It has fewer Bamboos, Orchids, and Aroids than other tropical areas; and, though two of its Palms (*Phœnix dactylifera* L. and *Elaëis guineensis* Jacq.) are familiar for their economic products, and the tribe *Borasseæ* is distinctively African, this group also is less well represented than it is either in Tropical Asia or Tropical America. Invasion from the east, presumably along the Mascarene bridge, has been more effective than from the north, and is represented in East Africa by the Indian *Gloriosa*, the palm liane *Calamus*, and, perhaps, by *Phœnix*.

One of the most marked facts connected with the flora of this continent is the wide range both in latitude and longitude of many of its species. No less than one-fifth of the Tropical species are common to East and West; whilst the range of the Trumpet- or Pig-lily (*Zantedeschia æthiopica* Spreng.), from Cape Town to the First Cataract of the Nile, is the botanical parallel of the wide latitudinal range of the Hippopotamus.

In East Africa a large area is occupied by Savannah-forest, in which occur scattered plants of *Euphorbia* and *Aloë*, with many herbaceous species; and by Thorn-forest, in which are numerous Acacias and Albizzias, with few herbaceous plants, but with many slender twining species and a few epiphytic forms of *Peperomia* and *Angræcum*.

In the west of the continent, on more retentive soil, we have the savannah of Loango, with lofty grasses, such as *Andropogon* and *Cymbopogon*, ten feet in height; a few low-growing shrubs, such as species of *Anona;* Palms, such as *Borassus flabellifer* L. and *Elaëis;* and the gigantic water-storing Baobab (*Adansonia digitata* L.). This passes southward into the stony deserts of the Kalahari Region that extend across the Southern Tropic, where Palms cease; but, with spinous Acacias and some bulbous species, in the loose sands occur the striking cucurbitaceous shrub the Naras (*Acanthosicyos horrida*

Welw.), with bitter foliage but aromatic gourds, and the even more remarkable *Welwitschia mirabilis* Hook. fil., a surviving isolated gymnospermous type.

MADAGASCAR.—Madagascar, separated from the continent by water nearly or more than 1000 fathoms deep, is considered as an ancient continental island. With seven months' rain, this tropical island is mainly covered by Rain-forest, with Tree-ferns, lianes, Bamboos, and epiphytic Orchids. The lofty granitic interior bears a savannah vegetation, and towards the south it is drier and more thorny. With a flora of over 4000 species, of which three-quarters, including one small order, the *Chlænaceæ*, are endemic, the *Compositæ* and Heaths suggest the generally African character of the flora, whilst the Bamboos and the Pitcher-plants (*Nepenthes*) connect it with the Indian Monsoon Region.

The granitic Seychelles, probably detached from Madagascar in Tertiary times, have also a considerable endemic element in their flora, of which the best known species is the remarkable Double Coco-nut (*Lodoïcea sechellarum* Labill.).

INDO-MALAYAN REGION.—In the Indo-Malayan or Indian Monsoon Region, with its mangrove-swamps and striking forms of *Ficus*, including the pillar-rooted Banyan (*F. indica* L.), the drip-tipped Pipal (*F. religiosa* L.), the Rampong or India-rubber (*F. elastica* Roxb.), and many others, we have the typical Rain-forest in Java, Ceylon, and the Malay states; but the less continuously wet Monsoon-forest over much of the rest of the area. In East Java, for instance, a non-retentive soil bears the tropophilous pure "djati" or teak-forests of *Tectona grandis* L. fil. Besides a profusion of epiphytic Orchids, Gingers and other *Scitamineæ*, and Bamboos, the many Water-lilies, the climbing Palms (*Calamus*), *Nepenthes*, and the *Dipterocarpaceæ* are characteristic.

In the north-west this region is succeeded at altitudes of over 5000 feet by what has been termed the Region of Rhododendrons. In the lower moister forests these large woody plants grow epiphytically; but at still greater altitudes they give place to conifers, such as *Picea Morinda* Link and *Cedrus Deodara* Loud., which extend to the upper limit of trees. So too, at similar altitudes in Java, forests of *Ficus* give place to Oaks,

and these are succeeded by *Podocarpus* and *Camelliaceæ* up to 9000 feet, where trees give place to shrubby *Vacciniaceæ*, such as *Thibaudia*, and to woody "everlastings" (*Gnaphalium*).

The eastward extensions of this region, marked by the occurrence of *Cycas*, which occurs also in Japan, of the various species of Nutmeg (*Myristica*), of Sandalwood (*Santalum*), and of such Palms as *Rhopalostylis* and *Kentiopsis*, are interesting as linking the flora of the south-east of the continent of Asia with tropical Australia, New Caledonia, the Fiji Islands, and even Juan Fernandez and Hawaii.[1]

TROPICAL AMERICA.—Neither in Africa nor in Asia is there as great a variety in the development of tropical conditions or as great a wealth of endemic types as in Tropical America. On the northern borders of the zone we have, in Southern Mexico and Central America, almost perennial rain, with the evergreen foliage, lofty trees, Tree-ferns, and numerous lianes and epiphytes of the true Rain-forest. Among the lianes the Palms of the genus *Desmoncus* replace the Asiatic *Calamus*, the Vanillas are among the many groups of endemic Orchids, and *Smilax* is represented by many species. The epiphytic Aroids *Anthurium*, *Monstera*, and *Philodendron*, and the *Bromeliaceæ*, among which is the Pine-apple (*Ananas sativus* Schult.), are peculiar to America, and some of the latter are epiphytic, whilst others are terrestrial. The Heliconias represent the *Scitamineæ* of India, and *Carludovica*, from the leaves of which are plaited the so-called "Panama" hats, with other *Cyclanthaceæ*, represent the Screw-pines. Many *Leguminosæ*, such as the Logwood (*Hæmatoxylon campechianum* L.), and *Cedrelaceæ*, such as the Mahogany (*Swietenia Mahagoni* Jacq.), are among the loftiest trees, the latter recalling the African Rain-forests of Senegal and Guinea.

The West Indies are but an insular extension of this

[1] Of the genus *Santalum* itself, *S. album* L. is Indian; *S. lanceolatum* R. Br., *S. obtusifolium* R. Br., and *S. ovatum* R. Br. are Australian; *S. austro-caledonicum* Vieill. belongs to New Caledonia; *S. Hornei* Seem. and *S. Yasi* Seem. are Fijian; *S. pyrularium* A. Gray and *S. Freycinetianum* Gaudich. are Hawaiian, the latter growing also in the Marquesas and Society Islands; and the related *S. fernandezianum* Phil. is represented apparently by one remaining tree in Juan Fernandez.

flora, differing, as does the Polynesian from the Indian flora, mainly by the greater profusion of Ferns and Orchids.

The northern shores of Colombia and Venezuela and the forests of Guiana serve to link the Central American Rain-forest with the vast area of the Amazon Region, for which the name Hylæa has been suggested. This region

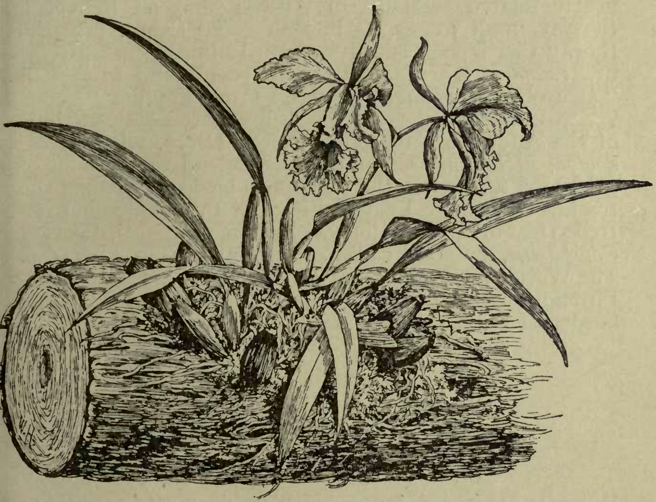

FIG. 9.—Epiphytic Orchid (*Cattleya*) in Brazil.
(*From Graebner's "Lehrbuch der Pflanzengeographie.*")

exhibits the greatest variety of Palms in the world. The *Lecythideæ*, a sub-order of *Myrtaceæ* comprising the lofty Brazil-nut (*Bertholletia excelsa* Humb. and Bonp.) and the Monkey-pots, the *Melastomaceæ*, *Piperaceæ*, and *Gesneraceæ*, the Passion-flowers, and the Begonias, are strikingly characteristic. The *Marcgraviaceæ*, peculiarly adapted to pollination by humming-birds, and many laticiferous *Euphorbiaceæ*, of which the Para Rubber-trees (*Hevea*) are the most important, are peculiar to this part of the region, where all the distinctive features of the Rain-forest are typically shown.

Where the winds have been deprived of their moisture by the mountains of Venezuela and Guiana, and the Serra do Mar in South-eastern Brazil, we get the savannahs known as "llanos" in Venezuela and as "campos" in Brazil. Here we have a marked alternation of wet and dry periods. Trees are few, but for a few Acacias, Anonas, and Cacti. The barrel-like "Barrigudos" (*Cavanillesia arborea* Schum.) represent the nearly related Baobabs of Africa; and on light soil the savannah passes, as in Bahia and Ceara, into the thorny Caatinga. South-westward almost pure groups of *Araucaria brasiliana* A. Rich. occur, and forests of "algarob," or *Mimoseæ*, extend into Paraguay.

ANDINE REGION.—On the well-watered eastern slope of the Andes, or Montaña Region, *Hevea*, with *Carludovica*, *Melastomaceæ*, and Palms extend to altitudes of over 3000 feet, when the Cinchonas begin; and then the treeless but grassy Eastern Sierra or Puna extends from 10,000 feet to the snow-line, with numerous Cacti, dwarfed *Compositæ*, spinous *Colletia*, and urticating *Loasaceæ*. The Western Sierra of Peru is even more barren, passing, through many degrees of latitude from the southern border of Ecuador, into absolute desert.

CHAPTER III

THE SOUTHERN ZONE

WIDELY separated for a considerable period, speaking geologically, the land-masses of the South Temperate Zone may each be considered as a *cul-de-sac* in which southward extension has been checked. Among the few links common to all we may mention the order *Proteaceæ* and the coniferous genera *Callitris* and *Podocarpus*.

SOUTH AFRICA.—Extending eastward and to the south of the Orange River from the Kalahari Region, the *South African Region* occupies a series of great plateaux or Karroos and steep slopes. The extraordinary variety of the vegetation is largely the result of the irregular distribution of the rainfall. There are no large or dense forests, no climbers, nor are trees or shrubs luxuriant.

The vegetation is mainly xerophytic. The Karroo-bush (*Acacia horrida* Willd.) is everywhere. In the west, wet winters and dry summers are accompanied by a typically sclerophyllous woodland, of which the Proteaceous Silver-tree (*Leucadendron argenteum* R. Br.) may be taken as a type. In the east, dry winters and a moist warm summer produce savannah conditions, forest-growth being restricted to the "kloofs" or river-valleys. The upper and middle karroos in the west (over 3000 feet and over 2000 feet respectively) bear small shrubby *Compositæ*, such as the Rhinoceros-bush (*Stœbe Rhinocerotis* L. fil.); and in August the middle terrace becomes luxuriantly green for a few weeks and is carpeted with blossoms of *Compositæ*, *Liliaceæ*, *Mesembryanthemum*, etc. The southernmost and lowest terrace, the "Bush," as it is termed, is, perhaps, the richest area for species—of its size—in the world. Cactus-like Euphorbias, Stapelias, Irises, *Gladiolus*, *Ixia*, Lilies and other bulbous plants, no less than 400 species of *Mesembryanthemum*, *Crassulaceæ*, such as *Crassula*, *Cotyledon*, and *Kalanchoë*, tuberous-rooted Pelargoniums, *Oxalis*, "everlastings," such as *Helichrysum* and many other *Compositæ*, terrestrial Orchids, such as *Disa*, and numerous species of *Aloë* are among the most characteristic. Just, however, as in Ireland we have luxuriant vegetation with few species, so here conversely the number of species by no means implies luxuriance.

The northern extension of this flora is of considerable interest. Various South African forms occur in the sub-alpine zone on the equatorial Kilima-njaro, a *Protea* and others in the Abyssinian Highlands, and many of these also on the Kameruns in the west. The South African affinity of the flora of the remote volcanic island of St. Helena is shown by the presence there—in an assemblage of 50 indigenous species of flowering plants and 26 Ferns, of the former of which 40 are endemic, 17 belonging to endemic genera, while 10 of the Ferns are also peculiar—of *Pelargonium* and *Mesembryanthemum*. The East India Company's goats and introduced plants have, however, nearly exterminated this native flora. *Pelargonium* also extends into Southern Europe and Asia Minor. Various species of *Erica*, *Lobelia*, *Gladiolus*, and other genera "more nearly allied to Cape species than they are to each other," with *Sibthorpia*, *Ulex*, *Genista*,

etc., extend to the Atlas, the west of the Iberian Peninsula, and so to Brittany and the west of the British Isles, whilst their susceptibility to frost prevents their extension eastward, away from the insular west-coast climate of the continent. These plants have been variously termed an Armorican, Asturian, Lusitanian, Iberian, or Atlantic flora.

Equally South African in affinity are the scanty floras of Ascension (7° S. lat.) Tristan d'Acunha (37° S.), Amsterdam (38° S.), and St. Paul (39° S.), of which the three first-named are connected by the South African rhamnaceous genus *Phylica*, and the three last-named by the grass *Spartina arundinacea* Carmich., although Ascension is separated from Tristan d'Acunha by 30° of latitude and the two small rocks of St. Paul and Amsterdam by 90° of longitude.

AUSTRALIA.—While northern Australia is tropical, with summer rains, and is practically an extension of the Indian Monsoon Region, between 19° and 29° S. a sub-tropical, trade-wind, desert region separates this area from the more distinctive south. In Tasmania, where rain occurs at all seasons, and in the "fern-gullies" of Victoria, which resemble the "kloofs" of Southern Natal, we have a Temperate Rain-forest, that, with Eucalypti, Acacias, and the evergreen *Fagus Cunninghamii* Hook., hung with the climbing grass *Tetrarrhena juncea* R. Br., is specially rich in Ferns. With the cosmopolitan Bracken (*Pteris aquilina* L.), the moisture-loving *Hymenophyllum tunbridgense* Sm., *Gleichenia*, and *Davallia*, are the arborescent *Dicksonia antarctica* Labill. and *Alsophila australis* R. Br. Most of the forests of east, south-east, and south-west Australia are of an open savannah type, although many of the Eucalypti, which are typically sclerophyllous and of a dreary glaucous hue, and constitute three-quarters of the forests, are exceptionally lofty trees (Fig. 10). These forests graduate into "scrub" with thickets of shrubby "Wattles" or Acacias; Proteads, such as *Grevillea*, *Hakea*, and *Banksia* , She-oaks (*Casuarina*), Epacrids, *Bursera*, and others; whilst the "Black-boys" or Grass-trees *Xanthorrhea* and *Kingia* grow, with the Cycads, on the borders of the grassy savannah of the interior (Fig. 11). This, which during the rainy season is adorned with numerous Lilies and other bulbs and terrestrial Orchids,

FIG. 10.—Forest of Eucalyptus in West Australia.
(*From Graebner's "Lehrbuch der Pflanzengeographic."*)

graduates into the sand-steppes or *Spinifex* desert and salt deserts of the driest regions

It is remarkable that the characteristic phyllodineous Acacias, *Eucalyptus* and *Melaleuca*, of Australia do not occur in New Zealand or New Caledonia.

In South America, south of the tropical forest area of Bolivia and North Argentina and the nitrate-desert of Atacama in Northern Chile, we have a counterpart of eastern Australia with its well-watered region between the ocean and the coast range, and the savannah and desert extending on the other side of the range. The range is, however, near to the western shore in America, to the eastern in Australia.

Of this extra-tropical Andine flora half the genera and four-fifths of the species are endemic, while no less than a quarter of the species belong to the *Compositæ*. The genus *Baccharis* alone is represented by 250 species. Representatives of the *Restiaceæ* and *Mutisiaceæ* suggest some remote connection with South Africa, while the characteristically Andine genus *Tropæolum* may be considered to represent the allied African *Pelargonium*. The *Loasaceæ* and *Larrea* extend northward to the Mexican area; *Fuchsia*, *Œnothera*, and *Heliotropium* are genera well developed also in Peru, or further north; whilst *Calceolaria*, *Fuchsia*, *Gunnera*, and *Acæna* extend to New Zealand, the Protead *Embothrium* to Australia, *Drimys* to New Zealand and Tasmania, and *Fitzroya* to Tasmania. *Libocedrus* ranges from California to New Zealand and New Caledonia.

CHILE.—In Northern and Central Chile much of the area is from 9000 to 18,000 feet above sea-level. Here, with *Calceolaria*, abundant in the Eastern Cordillera of Peru, is the home of *Escallonia*; and, in lower regions, where the climate resembles that of the Mediterranean, but with longer periods of drought, while spinous bushes predominate, some tropical forms remain, such as *Passiflora*, *Peperomia*, *Oncidium*, and *Tillandsia*.

PAMPAS REGION.—While this region gives place on the south to the Temperate Rain-forest of Valdivia, on the east of the Andes we have the varied conditions of the *Pampas Region*, which includes most of Argentina, Uruguay, Paraguay, and Patagonia. It is, on the whole, a dry region, thunderstorms and night dews being the chief forms of precipitation. Trees are, therefore, few

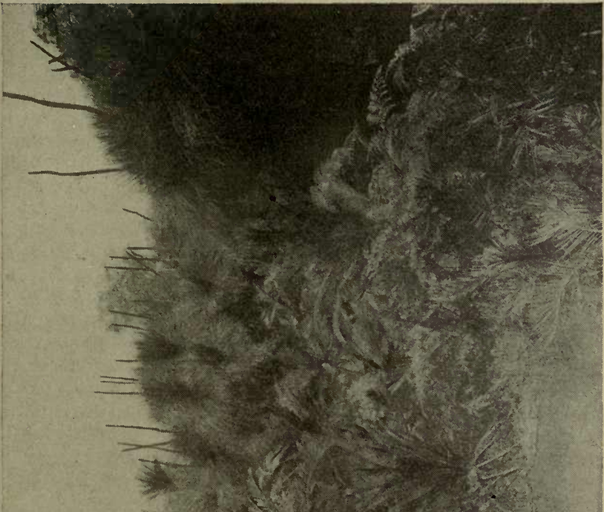

FIG. 11.—Grass-trees (*Xanthorrhea*), Cycads, and Ferns in West Australia.
(*From a photograph by W. Saville Kent.*)

in a wild state. In the north-west, however, where grasses do not flourish, the deeper-rooted bushy plants predominate. This thorn-savannah is known as the "Chanar" or "Espinal" region from *Gourliea decorticans* Gill., the "Chanar," a leguminous shrub, and an Acacia (*Prosopis alba* Gris.) known as "Espinillo." *Aspidosperma Quebracho* Schlecht. and species of Cactus are also characteristic. Further south, at the foot of the Andes, are "Las Salinas" of the Argentine, where vegetation is practically confined to a few woody and succulent *Salsolaceæ*. East of this lies the true pampas, a typical grassland, like the prairies of the west-central United States. A moderate rainfall, well distributed throughout the year and sufficient to keep the air moist during the vegetative period, though unsuited for trees is ideal for grass. The introduced Milk Thistle (*Silybum Marianum* Gärt.) and Cardoon (*Cynara Cardunculus* L.) have, however, ousted the Grasses over many square miles of area, forming impenetrable thickets.

About the parallel of 40° S., at the northern boundary of Patagonia, where the almost constant wind is from the north-west, *i.e.* is desiccated by the Andes, the grassland ceases, Grasses are represented by stiff dry species of *Stipa* and *Melica*, and the thorny shrubs of the north-west extend to the east coast.

On the other side of the Andes the *Antarctic Forest Region*, with a rainfall distributed throughout the year, brought by the north-west winds, and a milder climate than that of Northern Europe or the Alps, has many evergreen trees, although growth ceases in winter. In the north, including the island of Chiloë, the forests contain *Lauraceæ*, *Myrtaceæ*, and *Oleaceæ*, and even Bamboos and lianes, though not in the same abundance as in the tropics. In the south, in the tropophilous Beech forests of Fuegia, the evergreen *Fagus betuloides* Mirb. is succeeded by the "summer green" *F. antarctica* Forst. (the parasitic *Myzodendron* growing on both), and accompanied by *Drimys Winteri* Forst., *Berberis ilicifolia* Forst., and the ericaceous *Pernettya*, while the ground is carpeted with Liverworts, Mosses, and such Ferns as *Gleichenia acutifolia* and *Hymenophyllum pectinatum* Cav.

The presence at heights of 1800-3000 feet in Tierra del Fuego, 6500 feet in Valdivia, and 10,000 feet on

Aconcagua of such typical Antarctic species as the Tussock-grass (*Poa flabellata* Hook. fil.) and *Hierochloë redolens* R. Br., with the genera *Pernettya*, *Acæna*, and *Azorella*, suggests that they may have been driven northward and upward by an Antarctic Glacial Period.

In the low ground near the Straits of Magellan, as in the wind-swept Falkland Islands, forests give place to open peat-moors, with Rushes, Ranunculi, Cranberries, and Tussock-grass, which last extends to South Georgia. Among other characteristic species in the Falkland Islands are the Balsam-bog (*Azorella glebaria* A. Gray), a cushion-forming Umbellifer, the Red Crowberry (*Empetrum rubrum* Vahl), and the stunted *Myrtus nummularia* Poir.

Belonging to the same southern and treeless division of the Fuegian flora are the isolated islands of Kerguelen (49° S., 70° E.) and Marion (47° S., 40° E.), united by the remarkable endemic wind-pollinated crucifer *Pringlea antiscorbutica* R. Br. (Fig. 1), the tufts of the Fuegian balsam-bog *Azorella Selago* Hook. fil., and the cushions of *Acæna adscendens* Vahl, which ranges from Chile to New Zealand. Macquarie Island (55° S., 160° E.), with a treeless flora almost as impoverished as that of South Georgia, having but sixteen species of Phanerogams, also produces *Azorella Selago*, though it is, on the whole, more related to the south of New Zealand, as are the Auckland Isles (50° S., 170° E.) and Campbell Island (52° S., 170° E.), united by the handsome endemic asphodel *Chrysobactron Rossii* Hook. fil. They, however, have some low hills with stunted evergreen trees, including species of *Veronica*, the widespread myrtaceous *Metrosideros*, and the epacrid *Dracophyllum* which extends northward into New Caledonia. In spite of the persistent north-west winds of the "roaring forties" and the resultant Antarctic Drift, it is difficult to attribute the dispersal of species through these many degrees of longitude entirely to the ordinary or normal agencies of to-day. That a milder climate once prevailed, when plants may have passed from South America to New Zealand even by way of the Antarctic Continent, is indicated by lignites containing tree stems which occur on Kerguelen Land.

New Zealand.—Few floras are as interesting in their geographical affinities as is that of New Zealand. Form-

ing part of the "Australasian festoon," and built up of rocks of every geological period from Archæan to Pleistocene, this group of islands is clearly "continental" in origin. With a large proportion of the South Island occupied by Archæan schists, and a large proportion of the North Island covered by modern pumice and other volcanic rocks; with low sandy shores, and mountain-ranges rising far above a snow-line of about 3000 feet; with glaciers and boiling springs; there is almost every variety in edaphic conditions. Extending through thirteen degrees of latitude (34°—47° S.), the islands are, however, so narrow as to have a distinctly "insular" climate, although the rainfall is not high. Hard frosts are, in general, absent. The resultant flora is largely arborescent and evergreen, mesotherm, frigofuge, and hygrophilous, recalling the Temperate Rainforest of Southern Chile. Annual species and bulbs are very few in number. In dry situations a "scrub" occurs, composed largely of species of *Coprosma* and recalling the "maquis" of Southern Europe; and the development of sub-alpine xerophytes such as the cupressoid Veronicas and the hoary Mountain Daisies (*Celmisia*) is very striking. More general, however, even in the southernmost Stewart Island, is the forest. Ferns of all sizes abound. There are 138 species, from the arborescent *Cyathea* and *Dicksonia* to the delicate *Hymenophyllum*, of which there are twenty species. There are numerous epiphytes, and lianes, such as the "Bush lawyers" (*Rubus*), are also many, as in Chile. The flat-leaved Conifers (*Libocedrus*, *Podocarpus*, etc.), with the Papuan genus *Agathis*, belong mainly to the north, the Beeches to the south; but the latter are absent from Stewart Island.

The flora, comprising as it does about 1400 Phanerogams, is not rich in species; but no less than two-thirds of these are endemic. Of the remaining third the majority are common to Australia, indicating a common, if remote, origin for the two floras, though some forms with pappus-crowned fruits, such as *Olearia* and *Senecio*, may have been derived directly from Australia in comparatively recent times. On the other hand, 90 per cent. of the forest flora is stated to be of Melanesian affinities, a relationship interestingly exemplified in the distribution of the genus *Agathis*, and of the Nikau, the southernmost

of palms (*Rhopalostylis sapida* Wendl. and Drude), which, growing often under the shadow of the Kauri (*Agathis australis* Salisb.) in North Island, also extends, nearly 400 miles eastward, to the Chatham Islands. The arborescent liliaceous Cordylines, though mainly Indo-Malayan, are represented in South America; but *Phormium tenax* Forst., the New Zealand Flax, ranges only to the Auckland and Chatham Islands, another species of the genus occurring in Norfolk Island. The absence of Cycads from New Zealand emphasises the independence of the flora of direct connection with Australia. Of even greater interest is the Fuegian affinity of the flora, indicated by such species as *Acæna adscendens* Vahl and *Oxalis magellanica* Forst., and by no less than 56 genera present in New Zealand out of the total 84 of the Falkland Islands. But the great development of *Compositæ* (221 species, or about one-seventh of the entire flora), and such genera as *Gunnera, Fuchsia, Calceolaria,* and *Drimys,* may rather be termed Valdivian or Southern Andine than Fuegian characteristics. This evidence would seem to accord well with the theory of a Cretaceo-Eocene Antarctic bridge (the "Archinotis" of Dr. von Jhering) from Chile to New Zealand, New Caledonia, and Papua, while the Sub-antarctic or East Fuegian lowland forms may have spread eastward by a chain of islands at a later period.

BOOK IV

BOTANICAL ECOLOGY OR TOPOGRAPHY

WHILST the climatic conditions, upon which the floristic regions chiefly depend, are in the main uniform over the whole of those regions, the edaphic conditions commonly vary within much smaller areas. In the more minute or topographical study of plant-distribution it is, therefore, largely upon these edaphic conditions that we depend for the definition of smaller areas. In other words, among the factors which produce the vegetation of these smaller areas edaphic influences are the most effective or master factors. At the same time it must never be forgotten that climatic and edaphic factors combine to produce the vegetation. The greater prevalence of Ferns, for instance, in the west of Britain is due to the humidity of the air and not to any peculiarity of soil.

Ecology is the study of habitats, or environment, and the response thereto, as shown by the nature and characteristics of the inhabitants. The habitat is obviously the sum of all the external influences brought to bear on the organism.

Whilst in the broader study of plant-geography we constantly deal merely with the occurrence of species in various regions, so that a scarce plant is treated often on an equal footing with the commonest form, in this topographical study we are concerned rather with individuals, so that prevalent or "dominant" species which give a "physiognomy" or "facies" to the landscape are dealt with and the rarest occurrences are overlooked. This is sometimes expressed by terming ecology the study of vegetation; but, obviously, in this study it is impossible to separate the study of the environment from that of the vegetation that responds to it. The precise modes of action of such external conditions as salt, or lime, or humus, are questions for the physiologist. The external modifications of form resulting from various conditions, which we have already to some extent discussed, are of importance to the geographer because they influence the character of the landscape.

There is, in fact, no fundamental difference between that study of plant-form which we often style "adaptation" and the study of the collective "physiognomy" of vegetation.

ECOLOGICAL CLASSES.—An unnecessarily copious terminology has been coined to distinguish the various "ecological types" or "classes" of plants considered with reference to habitat. Many of these terms have been already alluded to; but it may be well to give a summary of the classes here, only premising that these groups neither comprehend all plants, nor are they entirely mutually exclusive.

Hydrophytes are divided into the floating Plankton and Pleuston, and the rooted Benthos, Plankton being microphytic, *i.e.* mostly Diatoms and Chlorophyceæ, and Pleuston megaphytic, comprising such Spermatophytes as *Hydrocharis*. Each subdivision is again divided according to whether it is represented by fresh-water or by marine plants. For example, among Benthos we have the *Nereid* formation, of Algæ attached to rocks, the *Enhalid* formation, of plants, such as *Zostera*, rooted in loose soil in salt water, and the *Limnæa* formation, the equivalent of the latter in fresh water including such plants as *Chara* and Water-lilies. Hydrophytes have, as we have seen (Book II. chapter x.) great mobility, especially by their methods of vegetative multiplication.

Helophytes, *Hemi-hydrophytes*, or Marsh-plants, include two marked formations, which have been named *Reed-swamp* and *Bush-swamp*. The former (Fig. 12) is characterised by tall Monocotyledons, such as *Phragmites*, *Typha*, and *Alisma*, often with creeping rhizomes, stiff elastic stems, but little branched and vertical leaves. The latter comprises the Alder-swamps so frequent in northern latitudes, the Cypress-swamps of *Taxodium* in the southern United States, and the thickets of *Nipa fruticans* Thunb. in the Indo-Malayan Region.

Hygrophytes are evergreen or sub-evergreen plants growing on moist soils and in constantly moist air, such as the bulk of those forming the Tropical Rain-forest. Shallow rooting and drip-tips to the leaves are characteristic features; and we may probably class here most *sciophytes*, or shade-plants, with thin leaves, stomata on both surfaces, and epidermal chlorophyll. The term

mesophyte, originally meant to apply to plants but little specialised in structure with reference to moisture, and flourishing in situations neither markedly wet nor markedly dry (of which perhaps, *po-ophytes* or meadow-plants are, perhaps, the most typical examples), has now been applied to more hygrophilous types, and many plants originally so called are now termed *tropophytes*.

FIG. 12.—Open reed-swamp association. *Scirpus lacustris* and *Castalia alba*. (*From photograph by Miss M. Pallis.*)

At the same time, even the sclerophyllous Holly and Spruce have been termed *mesophytes*. Perhaps our English Oak, Hornbeam, Hazel, and Hornbeam woods on clay or loam may be considered mesophytic; but all these constituent trees are *tropophytes*. This term was coined for those plants, including most of those of temperate regions, which, with thin deciduous leaves and rapid transpiration at one season, have corky bark and thick bud-scales to resist drought at another.

Xerophytes are plants adapted to a limited supply of physiologically available water. Most of their familiar structures, deep roots, thick cuticle or cork, enlarged or

fluted stems, and leathery or fleshy leaves, with few sunken stomata, are, therefore, adaptations to check transpiration or to store water. The drought to which they are subjected may be mainly due to climate, or mainly to soil. To the former master factor we may attribute the sclerophyllous, or leathery erect-leaved, vegetation of South Africa and much of Australia; the maquis of the Mediterranean; the chaparral of South California; the savannahs of Eastern Tropical Africa, of the Venezuelan llanos, and the Brazilian campos; the dry "patanas" of the interior of Ceylon; the "caatinga" or thorn-forest of many warm dry regions; and much of the steppe and desert areas of the globe. The soil of a desert is by no means necessarily sand, though generally non-retentive; but where precipitation is reduced to a minimum edaphic conditions are only of minor import. Xerophytic formations more directly due to soil have been grouped according to whether the soil is dry, or is only physiologically so. *Lithophytes*, Algæ, Lichens, and Mosses clinging to steep bare rock-surfaces prepare the soil for such phanerogamic *chasmophytes*, or crevice-haunting, species as Saxifrages or *Sempervivum;* and such *chomophytes* or rubble-dwelling types as *Sedum* are found alike on mountain "screes" and on maritime shingle-beds. Among *psammophytes*, plants of porous sands, we may class the marram-grass of the almost bare, drifting "white" dunes, the Sea-buckthorn (*Hippophaë*) and dwarf Willows of the more fixed "grey" ones, the Ling of more inland heaths, and by far the greater part of the coniferous forests of the world. The thick fronds of the Wall-rue (*Asplenium Ruta-muraria* L.), the small leathery leaves of the Rock-rose (*Helianthemum Chamæcistus* Mill.), and the distinctive hairiness of the Wayfaring-tree (*Viburnum Lantana* L.) serve to indicate that *calcicole*, or lime-dwelling, plants are decidedly xerophytic.

There are three marked ecological sub-classes of xerophytes which may grow in wet ground because the soil is to them physiologically dry. These are the *Bog-xerophytes* or *oxylophytes*, growing mainly in acid humus, such as *Sphagnum*, *Myrica Gale* L., *Eriophorum*, *Calluna*, and the insectivorous plants, *Drosera*, etc.; the majority of alpine plants or *psychrophytes*, growing in soil that is often so cold as to hinder root-absorption;

and *halophytes*, the plants of saline soils. Reference has before been made to the dwarf, tufted growth, evergreen leathery and hairy leaves, either cylindric ("juncoid"), adpressed ("cupressoid"), or inrolled, and the large bright flowers of alpines; and to the long roots, fleshy texture, and glaucous (blue-grey) bloom on the surface of many halophytes.

If the presence or absence of lime in the soil be a master factor, we may recognise a *calcifuge* class, including such a marked xerophyte as the Broom, as well as a mesophyte like the Foxglove, in opposition to the *calcicole* class above mentioned, which includes the Man-, Bee-, and other terrestrial Orchids, in addition to the species then named.

THE PLANT-ASSOCIATION.—In the study of vegetation a convenient and often most obvious unit is the *plant-association*, a community or aggregation of plants having a definite specific composition and a definite habitat, either with one social *dominant* species, or with several prominent ones. The former is termed a *pure*, the latter a *mixed* association. Some of our heaths consisting almost entirely of *Calluna* are good examples of pure associations, whilst in many copse associations two or three species are equally prominent (Fig. 13). For convenience of reference associations are named by the addition of the suffix *-etum* to the stem of the generic name of the dominant species, followed by its specific name in the possessive case. Thus a Pine-forest may be a *Pinetum sylvestris*, an Oak-wood a *Quercetum sessiliflorœ*.

PLANT-SOCIETIES.—Small aggregations of a non-dominant species within an association, due not to any noticeable differences in the habitat, but apparently to the gregarious habit of the species, such as spreading from one rhizome or self-sown from one parent, are known as *plant-societies*. Thus in a *Callunetum*, or heath consisting mainly of Ling (*Calluna Erica* L.), there may be patches or "societies" of *Erica Tetralix* L.

PLANT-FORMATION.—A group of associations on identical habitats, that is practically, the various communities in one region which inhabit the same soil, constitute a *formation*. On the sand-dune formation of a region, for instance, there may be *Cariceta arenariœ* and *Ammophileta arundinaceœ*, *i.e.* associations in which either *Carex arenaria* L. or *Ammophila arundinacea*

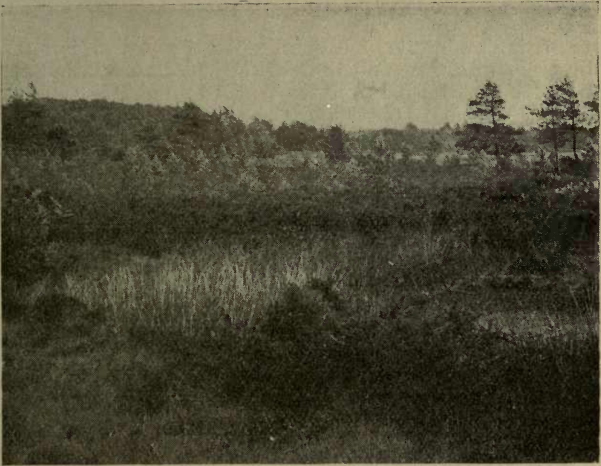

FIG. 13.—Oak-birch heath association. Birch, *Pyrus Aria*, Beech Heather, and Bracken. (*From photograph by S. Mangham.*)

FIG. 14.—Heath association invaded by *Pinus sylvestris*. Heather and Furze. Pool with *Potamogeton* and *Sphagnum*, surrounded by Rushes. (*From photograph by S. Mangham.*)

Host. is dominant. The name of a formation is made by the suffix *-ion*, and that of the chief association can be added in the possessive. A sand-dune being known as an *Arenarion*, a particular sand-dune may be *Arenarion Caricis-arenariæ*. For all the similar formations in the world the term *federation* has been proposed.

GUILDS.—Plants dependent upon others, such as lianes, epiphytes, saprophytes, and parasites, though they cannot well be dominant, may constitute a marked feature in an association. For societies of such plants the term *guild* has been suggested.

ZONATION.—Within the limits of one formation, progressive changes in habitat from place to place often produce a marked grouping of plants or associations in zones. A salt-marsh formation, for example, as traced from the sea landwards may exhibit in succession a *Salicornietum herbaceæ*, an *Atriplicetum*, a *Cakiletum*, and a *Triticetum juncei*, associations, that is, in which Glass-wort, Crab-weed, Sea-rocket, and *Triticum junceum* L. are dominant. Similar horizontal zonation is seen on the banks of rivers and ponds (Fig. 14). In forests, woods, and thickets a vertical zonation or succession of "storeys" may be traced. Thus we may have the "ground-storey," mainly occupied by cellular cryptogams, within two inches of the ground; the "field-storey," mainly composed of grasses and herbaceous plants, up to thirty-six inches; the "shrub-storey," and the "tree-storey." The seasonally complementary association of *Endymion*, *Pteris*, and *Holcus* previously mentioned (p. 57) may be considered as a form of vertical zonation.

TROPICAL FORMATIONS.—So potent are climatic influences that striking differences distinguish the associations and formations of the three or four great latitudinal regions. In most, however, woodland, grassland, desert, and shore are represented. The *Tropical Rain-forest*, in which the dominance of any one species can seldom be detected, is characterised, as we have seen, by a profusion of species, especially lofty evergreen trees with glossy leathery leaves, woody lianes, and epiphytes. Within the limits of the tropophilous *Monsoon-forest* local differences show themselves, as in the Bamboo-forest of the cloud-belt, the Sal forest of India, in which *Shorea robusta* Gaertn. is dominant, on permeable

FIG. 15.—Dry Oak-wood on sandy loam. Oak, Bracken, and *Holcus mollis*. (*From photograph by R. S. Adamson.*)

FIG. 16.—Interior of Beech-wood on chalk. (*From photograph by S. Mangham.*)

siliceous soil, and the Eng forest, on the ferruginous loam known as "laterite," with *Dipterocarpus tuberculatus* Roxb. Behind shelving sea-shores with what is still generally known as *Ipomœa Pes-capræ* may be thickets of *Barringtonia* ; or, especially in tidal waters, the prop-roots and pneumatophores, or aerating roots, of the oxylophytic Mangroves; or, in the Old World, *Nipa* and *Pandanus* ; or, on drier shores, *Spinifex squarrosus* L.

Warm Temperate Formations.—Among the mesotherm plants of the Sub-tropical and Warmer Temperate Zones the most noticeable formations are, perhaps, the various sclerophyllous communities to which some reference has before been made. In the maquis of the Landes of Bordeaux *Erica* is dominant; in Spain, the switch-like *Retama*, or, in the "jarales," *Cistus* ; whilst on the higher plateaux are the "tomillares," or scattered patches of "Tomillo" (*Thymus*). ~~*Prosopis* is dominant in the Californian "chaparral,"~~ and *Colletia* sometimes in the "espinal" of Chile, whilst in the Australian "scrub," "Mallee" (*Eucalyptus*), "Brigalow" (*Acacia harpophylla* F. v. M.), or other species of "Mulga" predominate locally. Whilst most xerophilous associations are "open," or sparse, the forests of evergreen oaks and of *Cedrus atlantica* Manetti in the Mediterranean area are "close."

Cool Temperate Formations.—In no regions have the formations been so thoroughly studied as in the Cooler Temperate Zone in Europe and North America. Among interesting points which have arisen are the relations of lime and acid humus to the woodland, where Oak and Birch and the Heaths characterise soils without lime which have acid humus (Fig. 15), and Beech woods and short-growing pasture grasses distinguish the chalk downs (Fig. 16).

In the Cold or Arctic Zone, trees dwindle to dwarf bushes, and the principal formations are the varieties of tundra.

Whether we study the geographical relations between the floras of wide regions or analyse with the minutest topographical detail the vegetation of the smallest areas, we are faced by an infinity of problems of climate, geology, soil, physiology, dispersal, evolution, and structural modification which demand painstaking observation and experiment.

BIBLIOGRAPHY

BAKER, J. G. Elementary Lessons in Botanical Geography. Lovell Reeve & Co., 1875. 110 pp. 8vo.

BOWER, F. O. The Origin of a Land Flora. Macmillan & Co., 1908. 727 pp. 8vo.

CLEMENTS, F. E. Plant Physiology and Ecology. A. Constable & Co., 1907. 315 pp. 8vo.

CLEMENTS, F. E. Research Methods in Ecology. Lincoln, Nebraska, 1905. 334 pp. 8vo.

DARWIN, CHARLES. The Origin of Species. John Murray, 6th edition, 1872. 458 pp. 8vo.

DE CANDOLLE, ALPHONSE. Géographie Botanique Raisonnée, Paris, 1855. 2 vols. 1366 pp. 8vo.

DRUDE, OSCAR. Manuel de Géographie Botanique, translated by Dr. G. Poirault. Paris, 1897. 552 pp. 8vo.

ENGLER, A. Versuch einer Entwickelungsgeschichte der Pflanzenwelt. Leipzig, 1879-82. Two parts, 588 pp. 8vo.

ENGLER, A. and DRUDE, O. Vegetation der Erde. Leipzig, 1896-1911. 13 vols. 8vo.

ERNST, ALFRED. New Flora of Krakatau, translated by Prof. A. C. Seward. Cambridge, 1909. 74 pp. 8vo.

GADOW, HANS. Geographical Distribution of Animals, in Darwin and Modern Science. Cambridge, 1909. pp. 319-336.

GRAEBNER, PAUL. Pflanzengeographie. Leipzig, 1909. 163 pp. 8vo.

GRAEBNER, PAUL. Lehrbuch der Pflanzengeographie. Leipzig, 1910. 303 pp. 8vo.

GREEN, W. LOWTHIAN. Vestiges of the Molten Globe. London, 1875. Part I. 8vo.

GRISEBACH, A. H. R. La Végétation du Globe, translated by Dr. P. Tchihatcheff. Paris, 1875-8. 2 vols. 1670 pp. 8vo.

GUPPY, H. B. Studies in Seeds and Fruits. Williams & Norgate, 1912. 528 pp. 8vo.

HALL, A. D. The Soil. John Murray, 2nd edition, 1908. 311 pp. 8vo.

HEMSLEY, W. B. Report on Insular Floras. London, 1885. 75 pp. 4to.

HERBERTSON, A. J. Outlines of Physiography. Edward Arnold, 1901; 2nd edition, 1907. 312 pp. 8vo.

HOOKER, SIR J. D. Botany of the Antarctic Voyage. London, 1844-60. 6 vols. 4to.

HOOKER, SIR J. D. Origin and Distribution of Arctic Plants. Linnean Society's Transactions, vol. xxiii. (1860). 97 pp. 4to.

HOOKER, SIR J. D. Lecture on Insular Floras. London, 1867. 36 pp. 8vo.

LYDEKKER, R. Zoological Distribution, in Encyclopædia Britannica, edition xi. vol. xxviii.

MOSS, C. E. The Fundamental Units of Vegetation. Cambridge, 1910.

REID, CLEMENT. The Origin of the British Flora. Dulau & Co., London, 1899. 191 pp. 8vo.

REID, CLEMENT. Palæobotany: Tertiary, in Encyclopædia Britannica, edition xi. vol. xxi.

SCHIMPER, A. F. W. Pflanzengeographie auf physiologischer Grundlage. Jena, 1898. Translated by Prof. W. R. Fisher, as Plant Geography upon a Physiological Basis. Oxford, 1903-4. 839 pp. 8vo.

SCOTT, D. H. Studies in Fossil Botany. A. & C. Black, 2nd edition, 1908-9. 676 pp. 8vo.

SCOTT, D. H. The Palæontological Record: Plants, in Darwin and Modern Science. Cambridge, 1909. pp. 200-222.

SCOTT, D. H. Palæobotany: Palæozoic, in Encyclopædia Britannica, edition xi. vol. xxi.

SCOTT, D. H. The Evolution of Plants. Williams & Norgate, 1911. 256 pp. 8vo.

SEWARD, A. C. Fossil Plants. Cambridge, 1898-1910. 2 vols. 1076 pp. 8vo.

SEWARD, A. C. Palæobotany: Mesozoic, in Encyclopædia Britannica, edition xi. vol. xxi.

SEWARD, A. C. Links with the Past in the Plant World. Cambridge, 1911.

SUESS, E. Das Antlitz der Erde. Leipzig, 1885-8. 3 vols. Translated by Dr. H. Sollas as The Face of the Earth. Oxford, 1904-8. 3 vols. 8vo.

TANSLEY, A. G. Types of British Vegetation. Cambridge, 1911. 416 pp. 8vo.

THISELTON-DYER, SIR W. T. Distribution of Vegetable Life, in Encyclopædia Britannica, edition ix. vol. vii. 1877. pp. 286-290, 4to.

THISELTON-DYER, SIR W. T. Plants: Distribution, in Encyclopædia Britannica, edition xi. vol. xxi.

THISELTON-DYER, SIR W. T. Geographical Distribution of Plants, in Darwin and Modern Science. Cambridge, 1909. pp. 298-318.

WALLACE, A. R. Island Life. Macmillan & Co., 2nd edition, 1895. 563 pp. 8vo.

WALLACE, A. R. The World of Life. Chapman & Hall, 1910. 408 pp. 8vo.

WARD, R. DE C. Handbook of Climatology. 1903.

WARMING, J. E. B. Œcology of Plants. Oxford, 1909. Edited by P. Groom and I. B. Balfour. 422 pp. 8vo.

INDEX

Acacias, 39, 100, 101, 103, 108, 113-116, 131
Acclimatisation, 35
Achillea, 54
Acrogens, 15, 18
Aërenchyma, 40
Africa, 108, 109, 112-114
Africa, South, 112-114, 125
Afro-South-American Bridge, 84
Agathis, 19, 120, 121
Agrology, 45
Alder-swamps, 123
Algæ, 90, 92-94
Algarob, 112
Aliens, 67, 68, 81
Alluvium, 46
Alpine plants, 29, 40, 126
Altitudinal zones, 1, 70-73, 88, 89
Amazon forests, 38, 111
America, Tropical, 110
American flora, 83
American, North, Desert, 104
Andine Region, 112, 116
Anemochores, 60, 65, 66
Anemophilous plants, 43, 60
Angiosperms, 15, 20
Antarctic connections, 84, 85
Antarctic Forest-region, 118
Anti-trades, 41
Ants and dispersal, 66
Aquatic plants, 33
Arch-Helenis, 84
Archinotis, 121
Arctic-alpine flora, 97
Arctic Region, 95-97
Arctis, 9
Area of distribution, 75
Armorican flora, 114
Ascension, 45, 114
Asian, Central, Desert, 103, 104
Asturian flora, 114
Atlantic Bridge, 83
Atlantic flora, 99, 114
Atlantis, 83
Atmospheric moisture, 35-39
Australia, 39, 114-116, 125

Bacteria, 50-52
Bad lands, 104
Ballast-plants, 61
Balsam-bogs, 39, 119
Bamboos, 72
Baobab, 39, 107, 108, 112
Barriers, 11, 74-78
Barrigudos, 112
Bathymetrical distribution, 93, 94
Beeches, 72, 85, 118
Beech-wood, 129, 130
Bennettites, 20
Benthos, 90, 92, 123
Birds and dispersal, 66, 70
Bolochores, 63
Brazil, 105-107, 111, 112
Bridges, 82-86 Brigalow 130
Britain united to Continent, 10
British flora, 80
Brongniart, 15
Buffon, 13
Burs, 66
Bush, 113
Bush-swamp, 123

Caatinga, 36, 105, 107, 125
Cacti, 39
Calcicole plants, 126
Calcifuge plants, 53, 126
Calciphobe plants, 53
Californian Region, 101, 102
Campos, 112
Cape Colony, 39
Carboniferous flora, 12, 18
Cardinal points of temperature, 32
Cardoon, 61
Censer-action, 63
Chanar region, 118
Chapparal, 101, 125, 130
Chasmophytes, 125
Chile, 116
Chino-Japanese Region, 98, 99
Chomophytes, 125
Cinchona, 112
Clay, 49
Climate, 2, 10, 27, 75; insular, 31
Climates, Continental, 31
Climatic regions, 5, 41
Close associations, 130
Cloud-girdle, 72, 89
Club-mosses, 14-19
Commensalism, 56
Complementary associations, 57

Continental climates, 31
Continents, Permanence of, 9, 82
Cordaïteæ, 16
Cretaceous flora, 21, 22
Critical temperatures, 32
Cromer Forest-bed, 24
Culm flora, 18
Cultivated plants, 2
Cushion-plants, 87
Cycadophyta, 19
Cycads, 16, 19, 20, 114, 121
Cypress-swamps, 123

Darwin, 82
Deserts, 37, 77, 100, 103, 104, 112
Devonian flora, 14-16
Dicotyledons, 20
Diluvium, 46
Dispersal, 62-70; occasional, 67, 81
Distance as barrier, 76, 77
Distribution-areas, 75
Distribution, Factors of, 27-94; harmonic, 81
Distribution of land and water, 4, 7
Doldrums, 41
Dominant species, 123
Draining, 61
Drude, 93
Dryads, 36

Earth's surface, 7
Earthworms, 52
Ecesis, 67
Ecology, 5, 122-131
Edaphic conditions, 45
Eluvium, 46
Endemic species, 5, 67
Enhalid formation, 123
Entomophilous plants, 60
Environment, 3; organic, 55-62
Eocene flora, 22
Epiphytes, 56, 111
Equatorial barrier, 11
Eriocaulon, 80
Espinal region, 118, 130
Eucalyptus, 114-116
Euphorbia, 108
Europæo-Siberian Region, 97, 98
Evergreen forests, 37
Evolution of plant-world, 7-26

Factors of distribution, 27-94
Fagus, 72, 85, 114, 118
Falkland Islands, 39, 119, 121
Federation, 127
Fenland, 52
Ferns, 45
Ficus, 109
Fireweed, 59
Fish and dispersal, 67
Floras, 4
Floristic geography, 5
Floristic Regions, 95-121
Föhn, 42
Formations, Tropical, 129
Fossil plants, 13-26
Frigofuges, 34
Fuegian flora, 80, 118, 121

Galapagos Archipelago, 79
Gelinden beds, 22
Geographical conditions, 4
Geological conditions, 4
Geophytes, 33, 34
Germination, Temperatures of, 33
Ginkgo, 16, 19, 98
Glacial Period, 12, 25, 26
Glossopteris, 19
Gondwanaland, 10, 19, 24
Grapple-plant, 66
Green, Lowthian, 8
Greenhouse plants, 2, 40
Greenland fossil flora, 21
Guilds, 128
Gymnosperms, 15, 20

Habitats, 5
Halophytes, 50, 100, 126
Hardy plants, 2, 40
Harmonic distribution, 81
Heat, 30-35
Heath flora, 59, 126, 128
Hekistothermic plants, 40
Heliophytes, 36
Helophytes, 123
Hevea, 111
Himalaya, 88, 89
Hooker, 88
Humboldt, 31, 88
Humus, 49, 50
Hydrochores, 64
Hydromegathermic plants, 39
Hydrophytes, 123
Hygrophytes, 38, 123
Hylæa, 111

Icebergs and dispersal, 67
Indigenous plants, 67

Indo-Malayan Region, 109, 110
Insect-pollination, 3
Insolation, 73
Insular climates, 31, 80
Island floras, 45, 78
Islands, 78, 83
Isotherms, 31

Japan, 98, 110
Jarales, 130
Java, 109
Juan Fernandez, 79
Jurassic flora, 12

Kalahari Region, 108
Kamerun, 113
Kamtchatka, 98
Karroos, 112
Kerguelen Land, 43, 44, 60, 79, 119
Kilima-njaro, 113
Krakatau, 45, 68-70

Lactoris, 79
Latitude, 2
Lepidium, 62
Levantine Region, 100
Lianes, 56
Light, 28-30
Lime, 49, 53
Limnæa formation, 54, 123
Lithophytes, 125
Llanos, 112
Loam, 49
Lodoicea, 65, 79, 109
Lusitanian flora, 114

Madagascar, 109 Mallee 130
Mangroves, 50, 51, 106, 107
Man's dependence on vegetation, 2; influence on vegetation, 61, 62
Maquis, 101, 120, 125, 130
Marattiaceæ, 17
Marine vegetation, 7
Marl, 49
Mediterranean flora, 100
Mesophytes, 38, 124
Mesothermic plants, 40
Mesozoic flora, 18-21
Mexican floras, 101, 102, 104
Mezquit, 101
Microthermic plants, 40
Miocene flora, 23, 83
Mobility, 59, 62
Moisture, 35-39
Monocotyledons, 20
Monsoons, 36, 42, 107
Moorland, 52
Mountain-chains, 72, 77
Mountain floras, 86-90
Mycorhizæ, 52, 53
Mulga 130
Nanism, 43
Nebular hypothesis, 8
Neocomian plants, 21
Nepenthes, 109
Nereid formation, 123
New ground, 57
New Zealand flora, 80, 85, 119-121
Nipa, 65, 107, 123
Nitrogen, 47

Oaks, 85
Oak-wood, 128, 129, 130
Ocean-basins, 9
Oceanic islands, 45, 82
Œningen fossil plants, 23
Oligocene flora, 23
Open associations, 130
Oreads, 36
Oxylophytes, 126

Palæozoic floras, 13-19
Pampas Region, 116
Parasites, 55, 56
Patagonia, 116, 118
Patanas, 125
Peat, 52
Permanence of continents, 9, 82
Peru, 112
Philotherms, 34
Physiognomy of vegetation, 5, 122, 123
Phyto-geography, 5
Plankton, 90, 92, 123
Plant-association, 126
Plant-formation, 126
Plant-life, Origin of, 13
Plant-society, 126
Pleuston, 92, 123
Pliocene flora, 23
Pneumatophores, 40
Podostemaceæ, 92
Polar origin of life, 13
Poophytes, 124
Potomac series, 21
Prairie Region, 100, 101
Precocious germination, 106
Pre-occupation, 3, 78
Primofilices, 17

Pringlea, 43, 44, 60, 119
Proteaceæ, 84
Psammophilous plants, 53
Psammophytes, 125
Pseudobornia, 15, 16
Psychrophytes, 126
Pteridophyta, 14-19
Pteridospermeæ, 16

Rainfall, 36
Rain-forest, 102, 105, 107, 109-111, 116, 123, 128
Reed-swamp formation, 123, 124
Regions of vegetation, 5, 95-121
Representation, 2, 80, 105
Rhododendron, 71, 89, 109
Rubber-tree, Para, 111
Ruderal plants, 60

Saharan Region, 103
St. Helena, 113
Salt, 50
Sand-dunes, 42, 59, 125
Santalum, 110
Saprophytes, 52, 56
Savannah, 37, 105, 107, 108
Saxicolous plants, 59
Scandinavian flora, 97
Schimper, 88
Sciophytes, 36, 124
Sclerophyllous plants, 39, 99, 125, 130, 131
Screes, 59, 125
Scrub-lands, 37, 120, 130
Sea as barrier, 76
Sea, Influence of, 31
Seasonal succession, 57
Sedum, 64, 125
Seed-dispersal, 3, 43
Seeds, Power of resistance of, 32
Selva, 36
Seychelles, 109
Shade-plants, 30, 124
Shore flora, 58, 59
Silicicolous plants, 53
Snow-line, 71
Social plants, 56
Soils, 32, 38, 45-55, 76
Sphagnum, 55, 76
Steppes, 37, 100
Storeys, 130
Stove-plants, 2, 39
Struggle for existence, 57
Succession, 54, 57-60
Succulent plants, 40
Sun plants, 29
Symbionts, 55

Tasmania, 114
Taxodium, 40, 123
Teak, 109
Tertiary flora, 22-26
Tetrahedral theory, 8
Thistles, 61, 66
Thorn-forest, 36, 105, 107-109
Tomillares, 131
Topography, Ecological, 5
Trade-winds, 41
Transport, 3, 4
Tristan d'Acunha, 114
Tropical Zone, 102-112, 129
Tropophytes, 38, 124
Tumble-weeds, 62
Tundra, 96, 130

United States flora, 98

Valdivia, 116, 118
Venezuela, 112
Viola, 54
Viviparous germination, 106

Wallace, 82
Water, 35-39, 47, 48; in soil, 4 ,
48
Water-plants, 90-94
Weeds, 61, 68
Welwitschia, 109
West Indies, 110
Wheat, 34
Wind, 40-45
Wind-witches, 62, 65

Xanthium, 61
Xanthorrhea, 114, 117
Xerophilous plants, 40, 104
Xerophytes, 38-40, 100, 105, 12

Yakutsk, 32
Yucca, 60

Zantedeschia, 108
Zinc, 54
Zonation, 58, 128-130; season 128; vertical, 128
Zone, Northern, 95-102; Trop cal, 102-112; Southern, 112-1
Zones of altitude, 1, 70-73; heat, 30; latitudinal, 30, 95
Zoochores, 66
Zostera, 93

35 net

Wales
Walcheren
Wallachia
Cornwall

Gallaria

p80 charact. of island floras ?

p 88-9 Rhod. distr.

Dasyl

Ipomoea